

Temperature, Light Regimes, and Harvest Time Shape the Total Volatile Content and °Brix/Acidity Balance of Strawberry Fruit (*Fragaria* × *ananassa* cv. Sonsation)

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Cite This: *ACS Agric. Sci. Technol.* 2026, 6, 1170–1184



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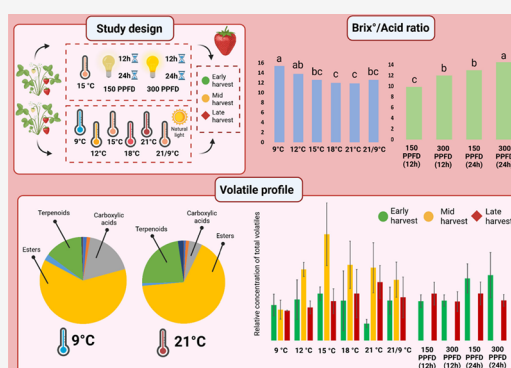
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ABSTRACT: The sensory appeal of strawberry (*Fragaria* × *ananassa*) depends on its chemical composition, including sugars, organic acids, and aroma-active volatiles. To investigate the effects of temperature and light conditions on fruit quality, strawberry plants (cv. Sonsation) were grown at six temperature regimes (9, 12, 15, 18, 21 °C, and 21/9 °C-day/night) and four combinations of light intensities (150 and 300 μmol/m²/s) and photoperiods (12 and 24 h/day). Yield, °Brix/acidity ratio and volatile compounds were assessed. °Brix increased with light intensity and photoperiod, while higher temperatures (15–21 °C) correlated with acidity. A favorable °Brix/acidity ratio correlated with both continuous light and high light intensity, as well as low ripening temperature. Volatile content peaked at 15 °C, and declined at 9 °C, proportionally elevating acids and reducing terpenoids. The findings indicate that extended high-intensity light can optimize sweetness and aroma in cv. Sonsation, whereas low temperatures benefit the °Brix-acidity balance but may reduce volatile compound development.

KEYWORDS: strawberry, *Fragaria* × *ananassa*, yield, flavor-related compounds, controlled environment, ripening conditions, temperature, light exposure



1. INTRODUCTION

Strawberries (*Fragaria* × *ananassa* Duch.) are highly valued by consumers across the world. The sensory attributes: flavor, aroma, and sweetness strongly influence consumer preference.^{1,2} These attributes are affected by a complex interaction between genetic, environmental, and agronomic factors.^{3–5} Understanding the individual factors influencing the sensory attributes is essential for advancing fruit quality. Due to its genetic diversity and adaptability, the strawberry plant is cultivated under a wide range of environmental conditions, exposing it to varying light and temperature levels during ripening.⁶ However, the ripening process of the strawberry fruit halts at harvest, limiting the potential to improve its post-harvest quality.⁷ This biological constraint underscores the importance of optimizing pre-harvest environmental conditions to enhance fruit quality.

In addition to genetic factors, environmental factors, particularly light and temperature, play a crucial role in determining strawberry fruit quality.⁵ Light intensity and photoperiod are shaped by factors such as latitude, altitude, season, time of day, cloud cover, and solar angle. At high latitudes, summer photoperiods can reach up to 24 h, while light intensity varies with atmospheric conditions and time of day.⁸ These factors

also impact the temperature experienced by plants, which in turn shapes their development and metabolism.

Strawberry cultivation is increasingly shifting from traditional open-field systems to controlled environments. This transition is driven by the growing unpredictability of weather patterns linked to climate change and a rising demand for sustainable food production with reduced pesticide use. As global temperatures rise and seasonal variability intensifies, understanding how light and temperature interact to influence flavor is becoming essential for optimizing cultivation practices and improving fruit quality under both current and future climatic conditions.

Strawberry flavor arises from a complex interplay between volatile and nonvolatile compounds that together shape the sensory experience. Nonvolatile compounds, primarily sugars and organic acids, contribute to sweetness and tartness, with the sugar-to-acid ratio serving as a key indicator of perceived sweetness.⁹ Volatile compounds, responsible for the fruit's character-

Received: November 25, 2025

Revised: June 4, 2026

Accepted: June 5, 2026

Published: June 27, 2026



istic aroma, are synthesized through multiple biosynthetic pathways and can be classified by their chemical structure.¹⁰ Flavor perception is often constrained by reduced levels of key volatiles such as esters, terpenoids, and lactones, as well as lower sugar concentrations³ and moderate acidity.¹¹ A sensory study demonstrated that sugar and acid levels strongly influence flavor ratings across most genotypes, while volatile compounds had limited impact.¹² However, one genotype with high sugar content but low ester levels received low flavor scores, suggesting that atypical volatile profiles can modulate the overall flavor experience. Notably, medium-chain fatty acid esters have been shown to significantly enhance perceived sweetness and consumer liking, independent of sugar content.³

Light intensity and photoperiod influence both the biosynthesis of sugars, organic acids, and volatile compounds in strawberry fruits.¹³ Light also affects the gene expression related to the biosynthesis of these compounds, thereby modulating the overall flavor profile.^{14,15} Temperature similarly influences both the physical and biochemical traits of strawberry fruits, including accumulation of volatile and nonvolatile compounds. While temperatures can enhance taste and aroma, extremes may cause physiological stress and reduce fruit quality.¹⁶ The interaction between light and temperature further complicates flavor development, as these factors can synergistically or antagonistically influence the metabolic pathways involved in production of taste and aroma compounds. Previous studies have shown that low ripening temperatures or temperature fluctuations between warm days and cool nights can improve the soluble solids content during fruit development.^{5,17,18} Cooler day/night regimes (18/12 °C) have been found to correlate with increased levels of fructose, glucose, citric acid, and ellagic acid compared to warmer combinations (25/22 and 30/22 °C) in strawberries of the cultivars Earliglow and Kent.⁵ Additionally, strawberries ripening at 15 °C have shown higher soluble solids content than those ripening at 22 °C.¹⁸

While notable research has been done on the effects of temperature and light on flavor-related compounds in strawberry fruit during the post-harvest stage,^{19,20} comparatively fewer studies have focused on the pre-harvest period, leaving current knowledge limited. Detailed investigations are needed to define optimal temperature ranges, light intensities, and photoperiod durations that optimize the accumulation of these compounds during fruit ripening. Moreover, beyond environmental influences, these traits are also cultivar-dependent.^{11,21,22} Despite growing insights into strawberry chemistry, the specific influence of pre-harvest temperature and light conditions on flavor development remains limited. To address these gaps and gain deeper insights into how environmental conditions influence fruit quality, controlled-environment experimental setups were conducted using cv. Sonsation. This cultivar was selected because it is a well-established, commercially important June-bearing strawberry cultivar in Norway, widely grown in both open-field and more protected production systems.²³ This makes it suitable for producing results relevant to commercial practice.⁸ Furthermore, despite the growing body of literature on strawberry aroma chemistry, little information is available for the cv. Sonsation, and its volatile composition or the influence of environmental factors have not been previously described.²⁴ The first experimental setup examined six distinct temperature regimes, while the second investigated combinations of photoperiod and light intensity, together providing an integrated and controlled approach to separate the effects of

temperature and light. By combining these complementary experiments, the study aimed to gain deeper insights into how temperature, light intensity, and photoperiod affect fruit yield, the accumulation of volatile compounds, and the levels of total soluble solids and organic acids throughout the harvest period. The primary objective was to determine the key environmental drivers shaping the flavor-related metabolic profile of cv. Sonsation, with direct relevance for optimizing fruit quality and consistency.

2. MATERIALS AND METHODS

2.1. Plant Material and Cultivation

Tray plants (250 cc, Kraege International, The Netherlands) of the strawberry cv. Sonsation were used in both temperature and light treatments. Transplants were potted on May 16 (W20) into 2 L containers filled with a 1:1 (v/v) mixture of peat and wood fiber (NORGRO, Norway) and cultivated in a greenhouse at 15 °C at the NIBIO Experimental Centre Holt, Norway (69°65'N, 18°90'E) until June 12 (W24). Plants were irrigated frequently with fertilized water (EC 1.5 mS cm⁻¹). A 1:1 mixture of Pioner Basis Red (7-5-27 NPK, Azelis, Denmark) and Calcinit (15.5-0-0 + 19% Ca, YARA, Norway) was applied until flowering, after which the ratio was adjusted to 60:40.

On June 12 (W24), plants were transferred outdoors for natural pollination, until July 5 (W27), when most flowers had developed into unripe fruit. During this period, all plants had natural temperature conditions with no precipitation. Subsequently, plants were randomly assigned to climate-controlled chambers with predefined temperature and light conditions at the Phytotron of the Arctic University of Norway, Tromsø. During the experimental period, senescent leaves and runners were manually removed. Plants were arranged on trolleys (0.5 m²), each holding four plants. The trolleys were randomly distributed across chambers and repositioned regularly to minimize positional effects. Biological pest control measures were implemented at the onset of treatment. The conditions in each sampling group and treatment are presented in Figure 1 and Table 1.

2.1.1. Temperature Treatments. The plants were grown at constant temperatures of 9, 12, 15, 18, 21, and 21/9 °C day/night (12 h/12 h) in daylight growth chambers. The temperatures were selected to cover a range of temperature scenarios, including diurnal variation. Natural daylength ranged from 24 h on July 5 to 17.4 h on August 15. After August 15, supplemental lighting (150 μmol/m²/s for 12 h daily) was introduced for the latest harvesting dates for the 9 and 12 °C treatments, to compensate for declining natural light and ensure comparable light exposure across treatments. Each temperature treatment consisted of four replicates, with nine plants per replicate. Temperature control in the phytotron was maintained within ±1 °C in the chambers, and a vapor pressure deficit of 530 Pa was applied across all growth chambers. Fully ripe fruits were harvested three times per week. Depending on the experimental temperature, the fruits were harvested in the period from W28 to W36. The time of start and end of harvest varied depending on the temperature regime.

2.1.2. Light Treatments. Plants were grown in dark chambers under four light treatments combining two light intensities (150 and 300 μmol/m²/s) and two photoperiods (12 and 24 h) with daily light integrals (DLI) of 6.48, 12.96, 12.96, and 25.92 mol/m²/d, respectively. These treatments represented both high and low light intensities, as well as intermediate DLI achieved through variation in photoperiod. Each light treatment consisted of four replicates with eight plants per replicate. Temperature was maintained at 15 ± 1 °C across all growth chambers, with a constant vapor pressure deficit of 530 Pa. The temperature of 15 °C represents an intermediate and agronomically relevant temperature for strawberry production under Nordic conditions. Previous controlled-environment experiments have shown that this temperature supports stable plant growth, allowing

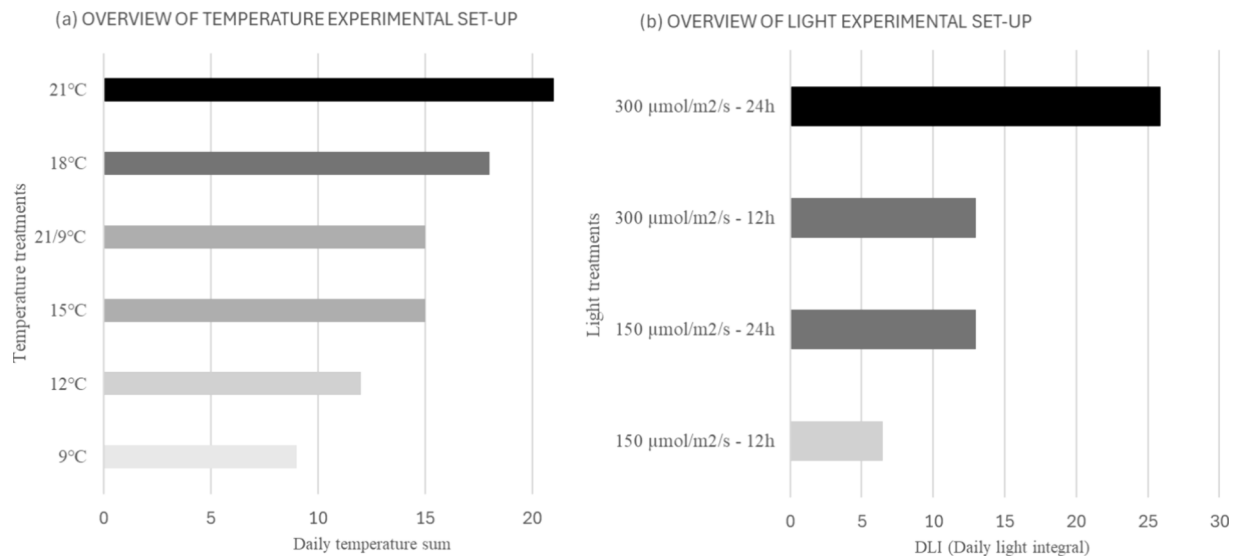


Figure 1. Overview of the temperature and light treatments, showing the individual treatments, their combinations, and corresponding daily temperature and daily light integrals.

Table 1. Overview of Experimental Treatments and Sampling, Including Temperature and Light Conditions, Harvest Time, and Harvest Week

treatment	harvest time	temperature	light conditions	week number of harvest
T09°C-early	early	9 °C	natural light	W32
T09°C-mid	mid	9 °C	natural light	W34
T09°C-late	late	9 °C	natural light	W36
T12°C-early	early	12 °C	natural light	W31
T12°C-mid	mid	12 °C	natural light	W33
T12°C-late	late	12 °C	natural light	W35
T15°C-early	early	15 °C	natural light	W30
T15°C-mid	mid	15 °C	natural light	W32
T15°C-late	late	15 °C	natural light	W34
T18°C-early	early	18 °C	natural light	W30
T18°C-mid	mid	18 °C	natural light	W32
T18°C-late	late	18 °C	natural light	W34
T21°C-early	early	21 °C	natural light	W29
T21°C-mid	mid	21 °C	natural light	W31
T21°C-late	late	21 °C	natural light	W33
T21/9°C-early	early	21/9 °C (12 h day/night)	natural light	W30
T21/9°C-mid	mid	21/9 °C (12 h day/night)	natural light	W32
T21/9°C-Late	late	21/9 °C (12 h day/night)	natural light	W34
L150-12h-early	early	15 °C	150 μmol/m2/s, 12 h/day	W31
L150-12h-mid	mid	15 °C	150 μmol/m2/s, 12 h/day	W34
L150-24h-early	early	15 °C	150 μmol/m2/s, 24 h/day	W31
L150-24h-mid	mid	15 °C	150 μmol/m2/s, 24 h/day	W34
L300-12h-early	early	15 °C	300 μmol/m2/s, 12 h/day	W31
L300-12h-mid	mid	15 °C	300 μmol/m2/s, 12 h/day	W34
L300-24h-early	early	15 °C	300 μmol/m2/s, 24 h/day	W31
L300-24h-mid	mid	15 °C	300 μmol/m2/s, 24 h/day	W34

light effects to be studied without confounding temperature stress.^{5,17,18} Fully ripe fruit were harvested three times per week over a five-week period from W30 to W35.

2.2. Measurements and Sampling

Throughout the harvest period, fruits were counted, weighed, and classified by size into two categories: >28 mm and <28 mm in diameter.

Fruit larger than 28 mm, having uniform size and quality, were sampled and stored at −20 °C for later chemical analysis. For the temperature treatments, three sampling weeks were selected (classified as early, mid, and late harvest time) with two-week intervals starting approximately in the second week of harvest (Table 1). For the light treatments, two sampling weeks were selected three weeks apart and classified as early and late harvest time (Table 1).

2.3. °Brix and Acidity

A Brix-acidity meter master kit (Atago, Japan) was used to measure the °Brix and acidity of the strawberry fruit, following the manufacturer's protocol. The °Brix/acidity ratio was then calculated. °Brix represents the weight of sucrose in 100 g of sucrose solution as a percentage by weight (Atago Co., Lt Multi Fruits Meter PAL-BX/ACID5, Tokyo, Japan). Thus, 1 °Brix is then the equivalent of 1 g sugar/sucrose in 100 g solution.²⁵

2.4. Volatile Compound Analysis with Headspace Solid Phase Microextraction Coupled with Gas Chromatography Mass Spectrometry (HS-SPME-GC-MS)

Approximately 50 g of frozen cv. Sonsation fruit was weighed into a beaker, and the same amount of 20% NaCl solution was added to enhance volatility of volatile compounds and prevent enzymatic activity and degradation of certain volatile compounds. The fruit was crushed and mixed with NaCl solution with a blender (Bamix, Switzerland) for approximately 90 s while still frozen. Two grams of strawberry mash were transferred to a 20 mL glass vial containing 10 µL of an internal standard mixture (4-methyl-2-pentanol 80.2 µg/mL in methanol). Three analytical replicates of each sample were prepared. All samples were analyzed on the same day they were prepared.

The samples were analyzed using HS-SPME-GC-MS. Volatile compounds were extracted from the headspace using a 2 cm DVB/CAR/PDMS fiber (50/30 µm, Supelco, Bellefonte, PA) at 45 °C for 30 min after 10 min of incubation. The fiber was conditioned at 230 °C prior to sample extraction. After extraction, the SPME fiber was immediately transferred to the injection port of a Trace 1310 gas chromatograph equipped with a TSQ 7000 EVO mass spectrometer (Thermo Fisher Scientific, Waltham, MA) to be thermally desorbed in the splitless mode at 220 °C for 3 min. A DB-WAX polar capillary column (60 m × 0.25 mm i.d. × 0.25 µm film thickness, J&W Scientific, Folsom, CA) was used to separate the volatile compounds. Helium was used as a carrier gas at a flow rate of 1.6 mL/min. The initial column temperature was set at 40 °C and held for 3 min, then increased to 220 °C at a rate of 5 °C/min and held at 220 °C for 10 min. Mass spectra were detected in the electron impact mode at 70 eV with a scan range from m/z 33 to m/z 300. The temperatures of the MS transfer line and the ionization source were set to 220 and 240 °C, respectively.

The retention indices of the volatile compounds were determined by co-injecting an alkane mixture (C7–C30, Sigma-Aldrich, St. Louis, MO). Volatiles were identified by comparing the obtained mass spectra with the NIST14 library and matching the RIs with those reported in the NIST Webbook that were obtained from studies under comparable experimental conditions.

Semi-quantification was carried out by dividing individual compound areas with the area of the internal standard and normalizing the values to be comparable to one gram of the strawberry-water mixture according to the following formula:

$$((a_{\text{peak}}/a_{\text{istd}}) \times (m_{\text{berry}}/m_{\text{NaCl}}))/m_{\text{sample}}$$

where

a_{peak} = area of compound peak

a_{istd} = area of internal standard peak

m_{berry} = mass of weighed strawberry fruit

m_{NaCl} = mass of weighed 20% NaCl-MQ-water solution

m_{sample} = mass of the analytical replicate

2.5. Statistical Analyses

Experimental data from °Brix and acid analyses and yield calculations were subjected to analysis of variance (ANOVA) by standard

procedures using a Minitab Statistical Software program package (Release 17.2.1 MiniTab, MiniTab Inc., State College, PA, USA). Tukey's test was used for the separation of means. Percentage values were always subjected to an arc sin transformation before the performance of the ANOVA.

SIMCA software (version 18.0, Umeå, Sweden) was used to perform principal component analysis (PCA) and partial least squares-discriminant analysis (PLS-DA) on the volatile data. Means and standard deviations of analytical and biological replicates were calculated with Microsoft Excel (Microsoft Corporation, 2024), and statistical analysis was carried out with IBM SPSS Statistics 29.0 (IBM Corp., Armonk, NY, USA). One-way ANOVA was used to assess differences in volatile data between treatment groups, followed by Tukey's Honest Significant Difference (HSD) test for post hoc pairwise comparisons (full results not shown). The significance level of $p < 0.05$ was considered statistically significant.

3. RESULTS AND DISCUSSION

3.1. Fruit Production

Fruit yield and size of cv. Sonsation were strongly influenced by temperature (Table 2). Yield and fruit size declined as temperature increased, with the lowest yield and the smallest proportion of large fruits at 21 °C. Cool (9–12 °C) and intermediate temperatures (15 and 21/9 °C day/night) were beneficial for producing a high number of large fruits. These results indicate that cool and intermediate ripening temperatures favor both higher yield and larger fruit size, whereas warmer conditions reduce both. The findings align with previous research emphasizing the sensitivity of strawberry development to temperature,^{5,26} although this sensitivity is cultivar-dependent.²⁷ Rising temperatures due to climate change may shorten crop cycles and affect overall productivity.

Yield and fruit size were also strongly affected by the photoperiod and total daily light-sum, but not by light intensity alone (Table 3). The treatment combining high light intensity and long photoperiod (300 µmol/m²/s, 24 h) produced the highest yield, the greatest number of large fruits (≥28 mm), and the largest average fruit weight. In contrast, the short photoperiod (12 h) treatments, particularly at the low light intensity (150 µmol/m²/s), resulted in significantly lower total yield and smaller fruits. Although increasing light intensity from 150 to 300 µmol/m²/s did not independently influence fruit characteristics, extending the photoperiod from 12 to 24 h improved both yield and fruit size. Overall, greater total daily light exposure increased productivity by enhancing both fruit number and size of cv. Sonsation. This is in line with a field study showing that seasons with longer daylength combined with higher total daily light exposure improve strawberry fruit yield and size.²⁸

3.2. °Brix and Acidity

Sugars, minerals, and organic acids account for the majority of soluble solids in strawberry fruit, with sugars primarily consisting of fructose, glucose, and sucrose.²⁹ Soluble solids content, as measured by °Brix, is considered an approximation of total sugar concentration and perceived sweetness, while acidity has been shown to correlate with sourness in strawberry fruit.^{12,30,31} Soluble solids content was found to have the highest correlation with sweetness and overall strawberry flavor,³ while strawberry genotypes with low soluble solids content were perceived as low in sweetness by a sensory panel.¹²

Table 2. Mean Fruit Yield (g), Number of Fruits Per Plant, and the Size Distribution Of Strawberry cv. Sonsation Ripened at Six Different Temperature Regimes (9, 12, 15, 18, 21, and 21/9 °C (12 h/12 h)) and the Proportion of Large Fruit, by Both Weight and Number, Relative to Total Yield for Each Temperature Treatment^a

temperature regime (°C)	fruits >28 mm diameter (per plant)		fruits <28 mm diameter (per plant)		total yield (per plant)		ratios	
	no.	g	no.	g	no.	g	>28 mm by weight	>28 mm by no.
9	16.7 ab	284 a	6.2 c	39 b	22.9 c	323 a	0.88 a	0.73 a
12	18.4 a	261 a	12.4 b	70 a	30.8 ab	332 a	0.79 ab	0.60 b
15	16.3 ab	202 bc	13.8 ab	71 a	30.2 ab	297 abc	0.68 bc	0.54 bc
21/9	18.5 a	233 ab	16.3 ab	77 a	33.7 a	314 ab	0.74 abc	0.53 bc
18	13.5 a	171 c	17.3 a	94 a	30.8 ab	264 bc	0.64 c	0.44 d
21	12.9 c	169 c	15.3 ab	72 a	28.3 bc	247 c	0.69 c	0.46 cd

^aValues are the means of four biological replicates (eight plants per replicate). Different letters within a column indicate significant differences between treatments ($p \leq 0.05$).

Table 3. Mean Fruit Yield (g) and Number of Fruits Per Plant and the Size Distribution of Strawberry cv. Sonsation Ripened under Four Combinations of Light Intensity (150 and 300 $\mu\text{mol}/\text{m}^2/\text{s}$) and Photoperiods (12 and 24 h) and the Proportion of Large Fruits by Weight and Number Relative to Total Yield for Each Treatment^a

light intensity ($\mu\text{mol}/\text{m}^2/\text{s}$) -daylength (h)	fruits >28 mm diameter (per plant)		fruits <28 mm diameter (per plant)		total yield (per plant)		ratio	
	no.	g	no.	g	no.	g	>28 mm weight	>28 mm number
300-24h	18.7 a	302 a	10.56 a	61.3 a	29.2 a	363 a	0.83 a	0.64 a
150-24h	14.4 b	223 b	10.63 a	60.2 a	25.1 a	284 b	0.79 ab	0.57 ab
300-12h	13.7 b	204 b	12.66 a	70.1 a	26.3 a	274 bc	0.75 b	0.52 b
150-12h	10.8 b	146 c	13.41 a	70.2 a	24.3 a	216 c	0.68 c	0.45 c
daylength	**	***	**	ns	ns	**	***	***
light intensity	ns	ns	ns	ns	ns	ns	ns	ns
DLI	***	***	*	ns	ns	***	***	***

^aValues are the means of four biological replicates (nine plants per replicate). Different letters within a column indicate significant differences between treatments ($p \leq 0.05$).

The °Brix values remained consistent in the cv. Sonsation fruits across the temperature treatments, while high acid levels correlated with high temperatures (15–21 °C), showing the lowest values at 9 and 12 °C (Table 4). This resulted in a higher °Brix/acidity ratio at lower temperatures, with the highest ratio observed at 9 °C (15.4) and the lowest at 21 °C (11.9). These findings suggest that acidity is more temperature-sensitive than sugar, and that cooler ripening conditions enhance perceived sweetness through a more favorable °Brix/acidity balance. This observation aligns with a previous study, which reported a negative correlation between temperature and the sugar/acidity ratio in strawberries of cv. Capri, with the ratio being primarily influenced by changes in acid content.³² Conversely, several studies have indicated that high temperatures negatively affect sugar content while increasing acidity in strawberries.^{5,18,33,34} Rising seasonal temperatures have been linked to reduced sweetness in field-grown cv. Festival strawberries.¹⁸ Similarly, a significant reduction in sugar content and sensory quality was reported for cvs. Albion and San Andreas ripening at 30/20 °C.³⁴ Additionally, both sugar and acid content decreased at high ripening temperatures (30/22 °C) in cvs. Earliglow and Kent.⁵

In contrast to the temperature treatments, the controlled light treatments influenced both °Brix and acid levels. °Brix values increased with cumulative light intensity, peaking under the highest light sum (25.92 $\text{mol}/\text{m}^2/\text{day}$) (Table 5) and were consistently higher under long-day light treatment (24 h),

compared to short-day conditions (12 h). Although acid levels were generally unaffected by changes in light intensity, the controlled light treatment resulted in a slightly lower acidity than the natural light treatment at 15 °C. As a result, the °Brix/acidity ratio increased in parallel with °Brix values, showing approximately a 30% rise under the highest light sum compared to the lowest. The highest ratios (14.5) were recorded under continuous light (24 h) and at the highest light intensity (300 $\mu\text{mol}/\text{m}^2/\text{s}$). These findings suggest that reduced light exposure during ripening may significantly lower the perceived sweetness of strawberries by decreasing sugar levels without affecting acidity. This result aligns with a previous study which observed shading to reduce sugar content without altering the citric acid concentration.¹³ As a result, the °Brix/acidity ratio was consistently higher in unshaded fruit compared to fruit grown under 47% shade. Another study found that light-exposed strawberries had higher °Brix and °Brix/acidity ratios, compared to nonexposed fruit, although this effect was cultivar-dependent.¹⁵ Thus, adequate light exposure during ripening is essential for enhancing the sweetness of the strawberry cv. Sonsation by increasing sugar accumulation and improving the °Brix/acidity ratio.

3.3. Volatile Compounds

A total of 104 volatile compounds were detected in the cv. Sonsation fruits through SPME-GC-MS. The compounds consisted of esters (59), aldehydes (11), carboxylic acids (10),

Table 4. Mean Values of Soluble Solids (°Brix, %), Total Acidity (% per 100 mL), and °Brix/Acidity Ratio in cv. Sonsation Strawberry Ripened under Six Temperature Regimes (9, 12, 15, 18, 21 °C, and Diurnal 21/9 °C) under Natural Light, Averaged across Early, Mid, and Late Harvests^a

temperature (°C)	°Brix (%)	acid (%/100 mL)	°Brix/acid ratio
9	10.70 a	0.68 b	15.7 a
12	9.80 a	0.70 b	14.0 b
15	10.12 a	0.82 a	12.8 bc
21/9	10.06 a	0.79 a	12.6 c
18	9.50 a	0.81 a	11.7 c
21	9.59 a	0.83 a	11.5 c

^aValues are the means of four biological replicates (nine plants per replicate) and three harvesting dates. Different letters within a column indicate significant differences between treatments ($p \leq 0.05$).

terpenoids (8), ketones (7), alcohols (6), furanone (1), lactone (1), and ether (1) (Table S1). A selection of volatile compounds with variable importance in projection (VIP) scores greater than 1 in the PLS-DA models (Figures S1–S3) is shown in Table 6. Normalized volatile data of individual samples, calculated as the mean of three analytical replicates, are presented in Table S2. Table S3 summarizes the means of biological replicates within treatment groups ($n = 4$), while Table S4 shows the total relative concentrations of volatile compound classes in each treatment group. For the temperature treatments, total volatile content in fruit reached its highest relative concentration during mid-season harvest, with the highest levels observed at 15, 18, and 21 °C (Figure 2). For the light treatments, highest relative total volatile content was detected in early season fruit (Figure 3). An exception was the lowest temperature treatment (9 °C), which had a consistently low volatile content during all harvest times. Fruit ripening at 15 °C and harvested in mid-season had the highest relative concentration in 52 out of the 104 detected volatile compounds, the majority of which were esters. In contrast, mid-season fruit at 9 °C had approximately four times lower total volatile content compared with fruit at 15 °C ($p < 0.05$). Another distinct outlier was the early-season fruit at 21 °C, which had the lowest total volatile content out of all experimental treatments, approximately four times lower than of mid-season fruit under the same temperature regime ($p < 0.05$).

Esters accounted for approximately 65% of the total volatile content in all treatments. The main ester groups identified were butanoates (20), acetates (13), and hexanoates (12), with methyl butanoate, ethyl butanoate, methyl hexanoate, and ethyl

hexanoate being the dominant esters. These four compounds represented 70–80% of the total ester content in cv. Sonsation and are consistent with previous reports identifying them as key contributors to strawberry aroma. Methyl butanoate and ethyl butanoate have been identified as having a significant positive correlation to strawberry flavor intensity.¹¹ Fruit from mid-harvest ripening at 15 °C had the highest relative concentration of the four main esters. In general, ester concentrations were the highest in fruit ripened at higher temperatures (15, 18, and 21 °C), with peak levels during mid-season, and were lower during early- and late-season harvests. At 9 °C, ester levels remained consistently low across all harvest times, and methyl 2-hexenoate was not detected under these conditions. Previous studies have shown that low post-harvest temperature conditions reduce the levels of esters such as methyl and ethyl hexanoates in strawberry fruit,³⁵ suggesting that similar low-temperature effects may be responsible for the reduced ester levels in the low-temperature treatment. The controlled light treatments revealed a slight correlation between photoperiod and total ester content: longer light exposure (24 h) enhanced ester levels compared to the shorter photoperiod (12 h). Specifically, fruit grown under low light intensity (150 $\mu\text{mol}/\text{m}^2/\text{s}$) had 1.2 times higher ester content under continuous light, while those under high light intensity (300 $\mu\text{mol}/\text{m}^2/\text{s}$) had a 1.5-fold increase. Low ester levels in early-season fruit and low-temperature ripening fruit from the temperature treatments may indicate an earlier perceived stage of ripening, as total ester concentrations have been shown to increase progressively during strawberry maturation.³⁶ This interpretation is further supported by patterns observed for mesifuran, a key furanone compound contributing to strawberry aroma that commonly increases during ripening.³⁷ Mesifuran levels were significantly higher ($p < 0.05$) in mid-season fruit ripened at 15, 18, and 21 °C compared to early-season fruit and fruit ripening at 9 and 12 °C. Exceptions to the general temperature response of esters included ethyl 3-methylbutanoate, propyl 3-methylbutanoate, and 3-methylbutyl 3-methylbutanoate, which showed the highest level at 9 °C and declined with increasing temperatures, reaching their lowest concentrations at 21 °C. Ethyl 3-methylbutanoate and other branched esters have previously been associated with reduced consumer acceptance,³⁸ while both ethyl 3-methylbutanoate and 3-methylbutyl acetate have also been identified as the predominant aroma volatiles in strawberry cvs. Kent and Mimac.³⁹ In contrast, ethyl pentanoate, 2-methylpropyl butanoate, ethyl 3-hexenoate, and 2-methylpropyl hexanoate had significantly higher concentrations ($p < 0.05$) in mid-season fruit ripening at 15 °C compared to all other treatments. Ethyl pentanoate has previously been highlighted for its strong association with

Table 5. Mean Values of Soluble Solids (°Brix, %), Total Acidity (% per 100 mL), and °Brix/Acidity Ratio Measured in cv. Sonsation Strawberry Ripened at 15 °C at Four Combinations of Light Intensity (150 and 300 $\mu\text{mol}/\text{m}^2/\text{s}$) and Daylengths (12 and 24 h), Corresponding to Three Daily Light Integrals (DLI), Averaged across Early and Late Harvest Times^a

light intensity ($\mu\text{mol}/\text{m}^2/\text{s}$)	photoperiod (h)	DLI ($\mu\text{mol}/\text{m}^2/\text{d}$)	°Brix (%)	acid (%/100 mL)	°Brix/acidity ratio
150	12	6.48	7.46 c	0.78 a	9.9 c
150	24	12.96	9.39 b	0.73 a	13.0 b
300	12	12.96	9.47 b	0.78 a	12.0 b
300	24	25.92	10.65 a	0.74 a	14.5 a

^aValues are the means of four biological replicates (nine plants per replicate), averaged across early and late harvests. Different letters within a column indicate significant differences between treatments ($p \leq 0.05$).

Table 6. Identification of Selected Volatile Compounds in Strawberry cv. Sonsation Detected Using HS-SPME-GC-MS^a

peak number	peak name	RI	RI NIST ^b	identification
esters				
2	methyl acetate	826	827	MS, RI
4	methyl propionate	908	906	MS, RI
7	methyl 2-methylpropanoate	922	919	MS, RI
13	methyl butanoate	984	983	MS, RI, STD
14	methyl 2-methylbutanoate	1008	1010	MS, RI, STD
16	2-propyl butanoate	1038		MS, STD
17	ethyl 2-methylbutanoate	1050	1042	MS, RI, STD
19	ethyl 3-methylbutanoate	1065	1067	MS, RI
20	butyl acetate	1069	1070	MS, RI, STD
22	methyl pentanoate	1081	1083	MS, RI
23	3-methyl-1-butanol acetate	1117	1126	MS, RI
26	methyl 4-methylpentanoate	1138		MS
29	propyl 3-methylbutanoate	1149		MS
34	methyl hexanoate	1182	1188	MS, RI
35	butyl butanoate	1213	1219	MS, RI, STD
38	butyl 3-methylbutanoate	1244		MS
41	unknown ester	1258		
42	3-methylbutyl butanoate	1261		MS
43	hexyl acetate	1268	1274	MS, RI
44	methyl heptanoate	1282	1279	MS, RI
46	methyl 2-hexenoate	1287		MS
47	3-methylbutyl 3-methylbutanoate	1290	1296	MS, RI
49	(3E)-3-hexenyl acetate	1302	1306	MS, RI
50	(3Z)-3-hexenyl acetate	1312		MS
53	(E)-2-hexenyl acetate	1328	1336	MS, RI
54	6-methyl-5-hepten-2-one	1334	1339	MS, RI
56	2-methylpropyl hexanoate	1348	1353	MS, RI
58	methyl octanoate	1384	1383	MS, RI
60	1-methylhexyl butanoate	1393		MS
62	butyl hexanoate	1407	1414	MS, RI, STD
63	hexyl butanoate	1410	1419	MS, RI, STD
64	hexyl 2-methylbutanoate	1422	1421	MS, RI
68	3-methylbutyl hexanoate	1454		MS
69	octyl acetate	1470	1458	MS, RI
76	octyl formate	1560		MS
80	hexyl hexanoate	1609	1612	MS, RI, STD
81	octyl butanoate	1616	1624	MS, RI
85	(2E)-2-hexenyl hexanoate	1671		MS
89	phenylmethyl acetate	1738	1726	MS, RI
93	octyl hexanoate	1818		MS
99	methyl cinnamate	2094	2071	MS, RI
101	cinnamyl acetate	2161	2150	MS, RI
carboxylic acids				
77	2-methylpropanoic acid	1568	1554	MS, RI
82	butanoic acid	1633	1642	MS, RI
86	2-methylbutanoic acid	1674	1674	MS, RI
91	pentanoic acid	1751	1743	MS, RI
94	hexanoic acid	1856	1860	MS, RI, STD
95	5-methylhexanoic acid	1926		MS
96	heptanoic acid	1974	1975	MS, RI, STD
102	nonanoic acid	2178	2171	MS, RI, STD
aldehydes				
21	hexanal	1077	1082	MS, RI, STD
36	2-hexenal	1215		MS
45	octanal	1284	1291	MS, RI
52	(E)-2-heptenal	1321	1318	MS, RI
59	nonanal	1389	1392	MS, RI, STD
72	decanal	1495	1496	MS, RI

Table 6. continued

peak number	peak name	RI	RI NIST ^b	identification
73	benzaldehyde	1525	1527	MS, RI, STD
74	(<i>E</i>)-2-nonenal	1536	1532	MS, RI
terpenoids				
31	β-myrcene	1154	1160	MS, RI
66	(<i>Z</i>)-linalool oxide	1444		MS
70	(<i>E</i>)-linalool oxide	1472	1471	MS, RI
75	linalool	1544	1549	MS, RI, STD
84	(<i>E</i>)-β-farnesene	1664	1664	MS, RI
90	α-farnesene	1750	1748	MS, RI
97	(6 <i>E</i>)-nerolidol	2047	2042	MS, RI
ketones				
12	2,3-butanedione	975	977	MS, RI
18	3-hexanone	1055	1050	MS, RI
24	3-penten-2-one	1125		MS
27	2,3-heptanedione	1144		MS
33	2-heptanone	1178	1184	MS, RI
alcohols				
28	1-butanol	1147	1150	MS, RI
57	1-hexanol	1352	1356	MS, RI
61	(<i>E</i>)-2-hexen-1-ol	1404	1409	MS, RI
71	2-ethyl hexanol	1487	1481	MS, RI
furanones				
79	mesifurane	1598	1580	MS, RI
lactones				
104	γ-dodecalactone	2375	2365	MS, RI

^aOnly compounds with the highest variable importance in the projection (VIP > 1) scores were included. ^bRetention index (RI) obtained from studies under comparable experimental conditions from NIST Webbook (<https://webbook.nist.gov/>).

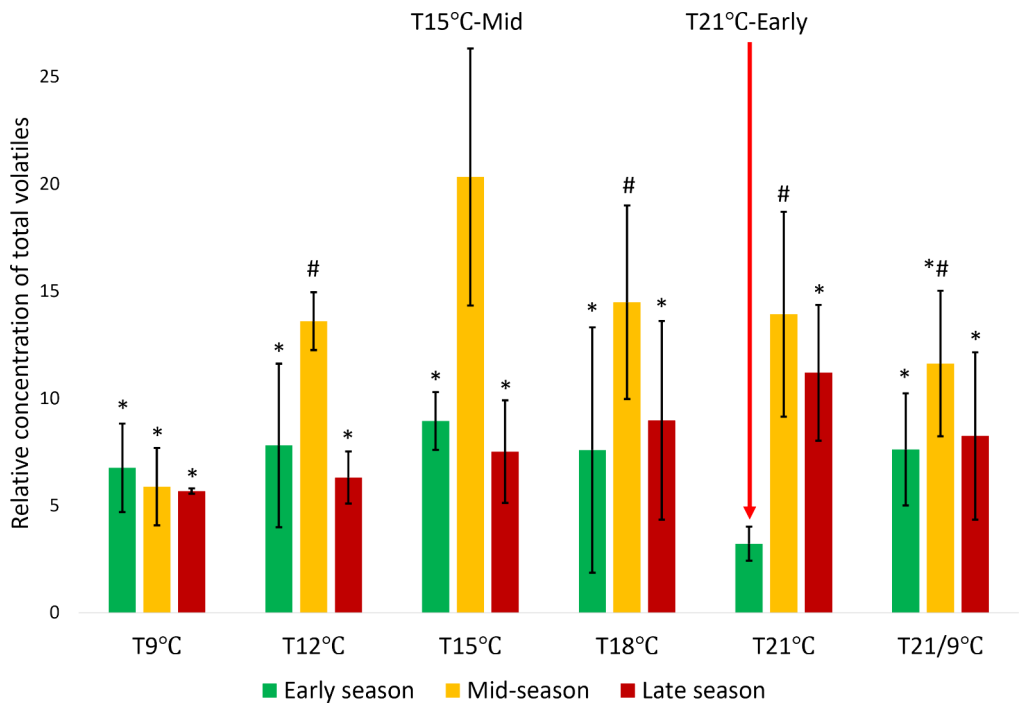


Figure 2. Mean total volatile content in strawberry cv. Sonsation fruit harvested at different time points (early, mid, and late season), ripened at six temperature regimes (T9°C, T12°C, T15°C, T18°C, T21°C, and T21/9 °C diurnal 12/12 h). The symbol * indicates a statistical difference from treatment T15°C-Mid ($p < 0.05$) and # indicates a statistical difference from treatment T21°C-Early ($p < 0.05$). Values represent means of four biological replicates, each with three analytical replicates.

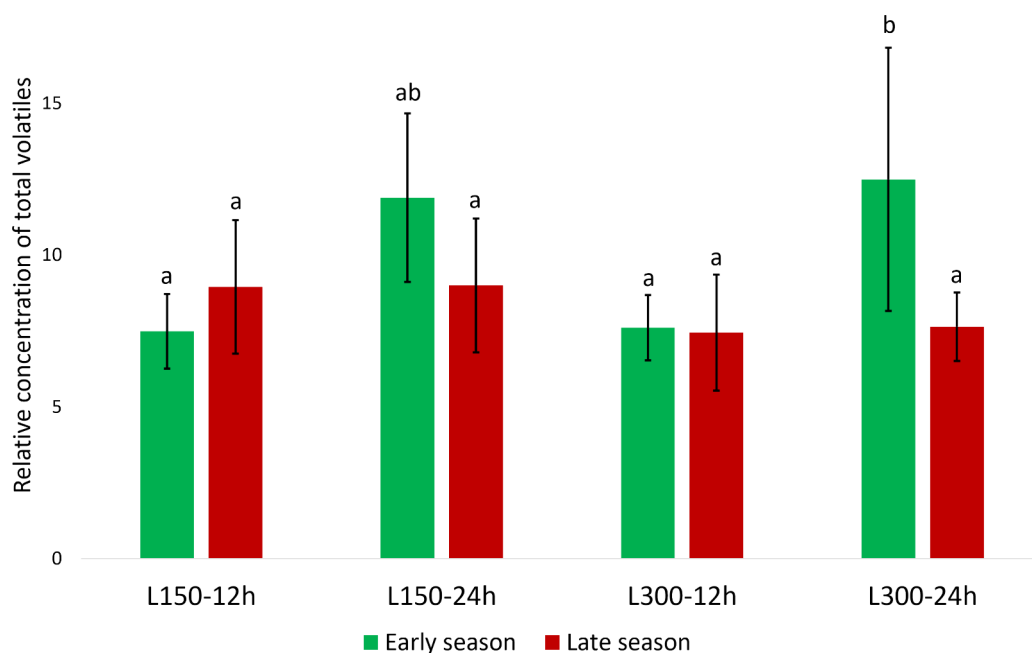


Figure 3. Mean total volatile content in strawberry cv. Sonsation fruit harvested at two different time points (early and late season), ripened at 15 °C under four light treatments (L150-12 h, L150-24 h, L300-12 h, and L300-24 h) combining two light intensities (150 and 300 $\mu\text{mol}/\text{m}^2/\text{s}$) and two photoperiods (12 and 24 h). Within each treatment, means followed by the same letter are not significantly different ($p \leq 0.05$). Data represents means of four biological replicates, each with three analytical replicates.

enhanced strawberry flavor, and its absence has been linked to less flavorful fruit.¹¹ Additionally, ethyl pentanoate has been found to be absent in half-red strawberries, suggesting an association with later perceived ripeness in mid-season.⁴⁰ Similarly, 2-methylpropyl butanoate has been identified as a marker of maturation, with its levels shown to increase significantly during fruit ripening.³⁶

Terpenoids were the second most abundant volatile group in cv. Sonsation fruit, accounting for approximately 20–28% of the total volatile content, except in the lowest temperature treatment (9 °C), where they accounted for only 14% of the total volatile content. Linalool and (6E)-nerolidol were the main terpenoids across all treatments and accounted for 94–97% of the total terpenoid content, consistent with previous findings identifying them as key terpenoids in cultivated strawberries.^{22,41} Similarly, the dominance of linalool and (6E)-nerolidol represented 97–100% of the total terpenoids in cvs. Benihoppe, Tochiotome, Sachinoka, and Guimeiren.⁴⁴ Both compounds have been positively correlated with flavor intensity in a study investigating 35 strawberry cultivars.¹¹ In the present study, both linalool and (6E)-nerolidol contents were lowest in fruit ripening at 9 °C and peaked in mid-season fruit at 15 °C, followed by 18 °C, 21/9 °C day/night regime, and 12 °C. Ripening at 15 °C led to approximately 3.2 times higher total terpenoid content compared to 9 °C ($p < 0.05$). The representation of terpenoids relative to the overall volatile content of cv. Sonsation fruit was relatively high (up to 28%), comparable to the cv. Tochiotome, where terpenoids represented approximately 30% of the total volatile content.⁴⁰ In contrast, terpenoids accounted for less than 1% of the total volatile content in the strawberry cvs. Korona and Polka, and 12% in cv. Honeoye.⁴² The production of both linalool and (6E)-nerolidol has been linked to the presence of the FaNES1 allele, which is

common in cultivated *F. × ananassa* cultivars, while absent in diploid, tetraploid, or hexaploid species, such as *F. vesca* (wild strawberry), *F. orientalis*, or *F. moschat*.⁴³ Given that linalool and (6E)-nerolidol are highlighted as important compounds regarding the overall strawberry aroma,^{11,38} their elevated levels in cv. Sonsation suggest it has favorable aroma related quality attributes.

Volatile acids comprised approximately 5–8% of the total volatile content across most treatments, with notable proportional increases to 13% at 12 °C and 18% at 9 °C. These proportional increases were primarily due to decline in esters and terpenoids. Hexanoic acid and 2-methylbutanoic acid were consistently the most abundant acids, in agreement with previous reviews,⁴⁴ followed by 2-methylpropanoic acid and butanoic acid. An inverse relationship was observed between temperature and the relative concentration of most volatile acids, particularly butanoic acid and 5-methylhexanoic acid, both peaking at 9 °C and declining with increasing temperature. In contrast, fruit ripening at 21 °C had consistently low volatile acid levels across all harvest times, except for acetic acid, which was more abundant at higher temperatures, peaking at 18 and 21 °C.

Further characterization of the volatile composition of the different treatment groups was performed by using multivariate analyses. The PCA model did not reveal clear separation between treatments, indicating an overall similarity in their volatile composition (Figure S4). In contrast, the PLS-DA model demonstrated improved separation, particularly in distinguishing the lowest temperature treatment (9 °C), which was clearly separated from all other treatments (Figure S5). This separation suggests that ripening at 9 °C resulted in a more distinct volatile composition compared to fruits ripening at higher temperatures. Meanwhile, the remaining nine treatments clustered together, reflecting a higher degree of similarity in their volatile

composition. The results highlight the possible sensitivity of the cv. Sonsation strawberry aroma composition to low-temperature ripening, which may lead to a unique but less complex volatile composition compared to those developed under warmer conditions.

For the final PCA models, only volatile compounds with VIP scores greater than 1 were selected. A PCA of the temperature treatments revealed a separation between mid-season fruit and other harvest times as well as a separation between the highest and lowest temperature treatments (Figure 4). The first two principal components (PC1 and PC2) explained 66.2% of the total variation, with PC1 and PC2 accounting for 44.0 and 22.2%, respectively. Along PC1, the treatments were grouped and differentiated by harvest time, with mid-season fruit clustering on the far-right side of the score plot, while most of the early and late-season fruit appeared on the left side. In contrast, temperature treatments were divided along PC2, with low-temperature treatments (T9°C and T12°C) located on the positive side, and high-temperature treatments (T21°C and

T18°C) on the negative side. The two temperature treatments with the identical daily sum of 15 °C (T21/9 °C and T15°C) were not clearly separated in the model, clustering between the low and high temperature groups. Ketones and acids such as butanoic acid, hexanoic acid, 3-hexanone, and 2,3-butanedione were associated with lower temperature treatments, while most methyl esters, including methyl butanoate and methyl hexanoate, correlated with higher ripening temperatures. Based on their VIP score, 5-methylhexanoic acid (VIP = 1.74) and 2,3-butanedione (VIP = 1.62) were most influential compounds in discriminating between temperature treatments and were strongly associated with low temperature ripening (Table S5). These findings align with the overall volatile composition where lower temperatures (9 and 12 °C) promoted an overrepresentation of acids and ketones due to reducing levels of terpenoids and certain esters. Terpenoids accounted for approximately 25% of the total volatile content in other temperature treatments, but this proportion decreased to 14% at 9 °C. In contrast, the relative acid content was increased to

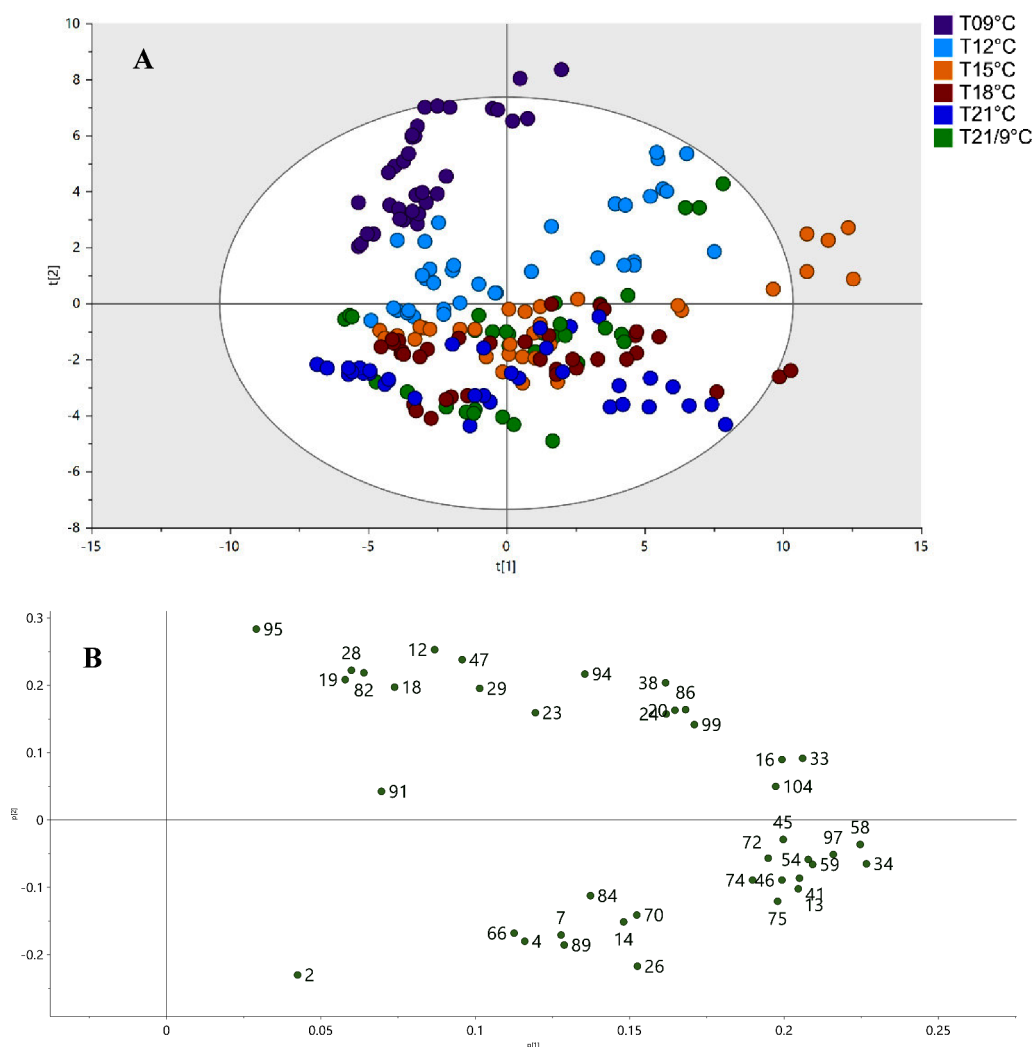


Figure 4. PCA of relative concentrations of volatile compounds in strawberry cv. Sonsation fruit ripening at six temperature regimes (T9°C, T12°C, T15°C, T18°C, T21°C, and T21/9 °C diurnal day/night 12/12 h). (A) Score plot based on the first two principal components. Values represent four biological replicates, with each data point in the score plot corresponding to an analytical replicate ($n = 3$). (B) Loading plot based on the first two principal components. Only volatile compounds with the variable importance in the projection (VIP) scores > 1 were included in the PCA model. Compound numbers refer to Table 6.

18% at 9 °C, compared to only 5% at 21 °C. Notably, hexanoic acid and 2,3-butanedione, in particular, are known as contributors to off-flavor in strawberries; hexanoic acid is associated with sour or rancid-like off-flavors,^{45,46} while 2,3-butanedione may contribute to a buttery or rancid-like off-flavors.⁴⁷ Given the known role of esters and terpenoids, such as methyl butanoate, linalool, and (6*E*)-nerolidol, in enhancing strawberry flavor and perceived sweetness independent of sugars,^{3,11} their reduced presence alongside an increased proportion of volatile acids at low temperatures is likely to impair sensory characteristics and diminish overall flavor quality.

A PCA model of controlled light treatments (L150-12 h, L150-24 h, L300-12 h, and L300-24 h) did not reveal a clear separation based on light intensity. Instead, clustering was observed based on photoperiod and harvest time, with PC1 and PC2 accounting for 40.7 and 21.7% of the total variation,

respectively (Figure 5). Most late-season fruit clustered on the negative side of PC2 in the score plot and were associated with alcohols and acids, including (*E*)-2-hexen-1-ol, 1-hexanol, butanoic acid, and 5-methylhexanoic acid, as well as methyl cinnamate and cinnamyl acetate. Among these, (*E*)-2-hexen-1-ol was the most influential in discriminating between groups, with a VIP score of 1.82 (Table S6). Early-season fruit was separated along PC1 based on photoperiod, with the 24 and 12 h treatments located on the negative and positive side of PC1, respectively. Overall, early-season fruit exposed to continuous light (24 h) exhibited a slightly higher total volatile concentration compared to the short-day treatment (12 h), showing a strong correlation with butanoate and hexanoate esters such as methyl hexanoate, 3-methylbutyl hexanoate, and 2-methylpropyl hexanoate. However, this separation was not distinctly pronounced, due to overlap between treatments. The slightly lower volatile

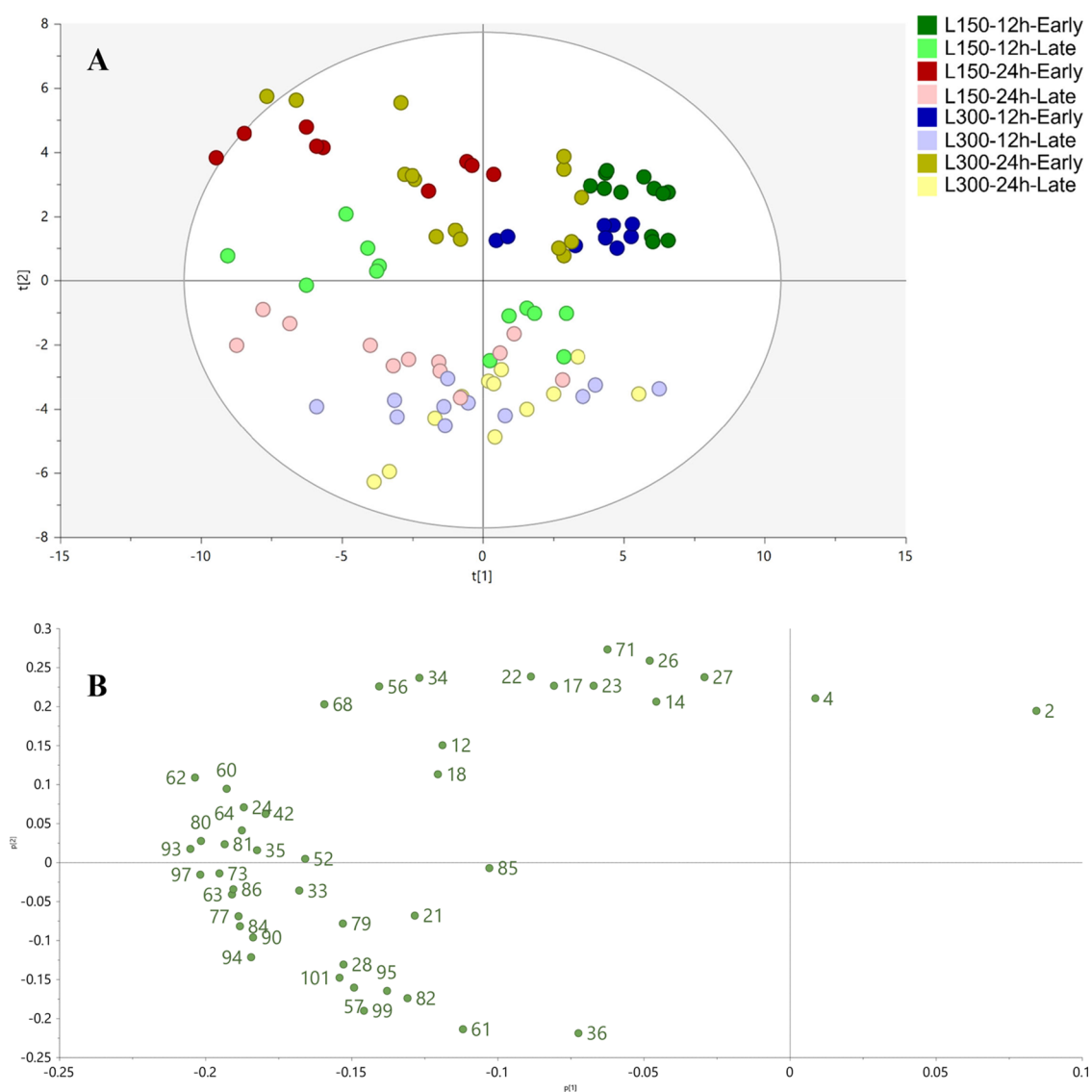


Figure 5. PCA of relative concentrations of volatile compounds in strawberry cv. Samsung fruit ripening at four light treatments (L150-12 h, L150-24 h, L300-12 h, and L300-24 h) combining two light intensities (150 and 300 $\mu\text{mol}/\text{m}^2/\text{s}$) and two photoperiods (12 and 24 h), harvested at two timepoints (early and late). (A) Score plot based on the first two principal components. Data represents four biological replicates, with each data point in the score plot corresponding to an analytical replicate ($n = 3$). (B) Loading plot based on the first two principal components. Only volatile compounds with the highest variable importance in projection (VIP) scores > 1 were included in the PCA model. Compound numbers refer to Table 6.

levels in fruit ripening under the shorter daily photoperiod may be explained by the same mechanisms seen in shading studies,¹³ where reduced light exposure is shown to negatively affect several aromatic volatiles, such as hexanal, hexenal, ethyl methyl butanoate, and methyl butanoate.¹³ In contrast, fruit exposed to continuous light (24 h) experienced no shading period, which may have contributed to their enhanced volatile content. These results suggest that photoperiod plays a more influential role than light intensity in shaping the volatile composition in strawberries of cv. Sonsation, with continuous light exposure potentially enhancing aroma-related compounds and improving overall flavor quality.

To further compare the effect of controlled light with natural light, the 15 °C treatment from the temperature setup (T15°C) was compared with the controlled light treatments (L150-12 h, L150-24 h, L300-12 h, and L300-24 h) using PCA (Figure 6).

The model showed a slight separation of natural light and controlled light treatments, which separated along PC2, while PC1 and PC2 explained 42.2 and 18.1% of the variance, respectively. Controlled light treatments clustered on the negative side of PC2, correlating with terpenoids typical of wild strawberry clones,²² including α -farnesene, (*E*)- β -farnesene and β -myrcene. The strongest correlation with controlled light was observed for α -farnesene and (*E*)- β -farnesene, both of which had a VIP score of 2.17 (Table S7). In addition, the controlled light cluster correlated with hexyl and hexenyl acetates, including (*E*)-2-hexenyl acetate, (3*E*)-3-hexenyl acetate, (3*Z*)-3-hexenyl acetate, and hexyl acetate. A high proportion of acetate esters in *F. vesca* was linked to a more floral aroma compared to *F. × ananassa*.⁴⁸ Furthermore, since the light quality and duration have been linked to the promotion of ripening and enzymatic pathways involved in the formation of acetate esters,

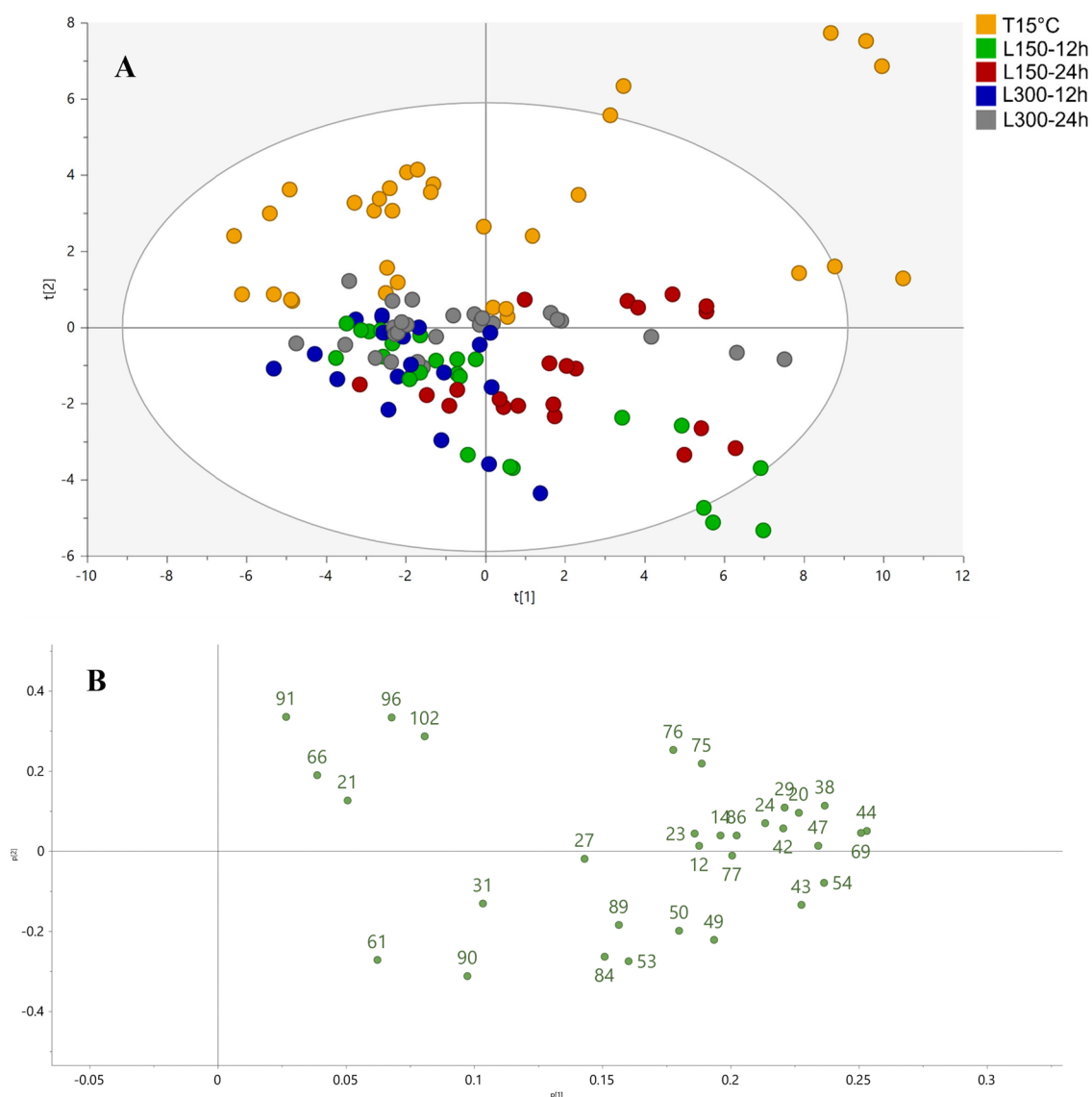


Figure 6. PCA of relative concentrations of volatile compounds in strawberry cv. Sonsation fruit ripening at 15 °C under natural light (T15°C) and in controlled light treatments (L150-12 h, L150-24 h, L300-12 h, and L300-24 h) combining two light intensities (150 and 300 $\mu\text{mol}/\text{m}^2/\text{s}$) and two photoperiods (12 and 24 h). (A) Score plot based on the first two principal components. Values represent four biological replicates, each data point in the score plot representing an analytical replicate ($n = 3$). (B) Loading plot based on the first two principal components. Only volatile compounds with variable importance in the projection (VIP) scores > 1 were included in the PCA model. Compound numbers refer to Table 6.

it is possible that ripening under continuous light promoted the formation of these esters.^{49–51} Notably, hexyl acetate has been highlighted as a key contributor to the overall consumer acceptability and appreciation of strawberry fruit.^{10,52} (*E*)-2-hexen-1-ol, which showed a strong association with the 12-h photoperiod, has been reported to be abundant in the strawberry cv. Clery during the over-ripe stage,³² whereas a decrease during ripening was observed in the strawberry cvs. Carezza, Darselect, and Marmolada.³⁶ In contrast, fruit ripening under natural light (T15°C) correlated with pentanoic, heptanoic, and nonanoic acid, which were entirely absent from controlled light treatments, as well as linalool, a terpenoid associated with cultivated strawberries.⁴¹ Although fruit ripened under natural light (T15°C) was partially separated from the controlled light cluster, it did not form a well-defined grouping due to the high variability in the volatile concentrations between early-, mid-, and late-season harvests. In contrast, the volatile compound content of fruit ripening under controlled light had less variation between harvest times, likely due to the stable light environment and no variations in light intensity and light spectrum. The greatest temporal variation in total volatile content was observed in fruit ripening under natural light at 21 °C, where mid-season fruit had approximately four times higher volatile content than early-season fruit. In addition to variations in light intensity, this effect may reflect accelerated ripening at higher temperatures, resulting in earlier harvest once visual ripeness is attained, possibly prior to peak volatile accumulation. A similar, though less pronounced, decreased volatile compound content during the early-season harvest fruit was also observed for other temperature treatments (12, 15, and 18 °C), suggesting less time for volatile compound accumulation. Overall, these findings highlight that more controlled light conditions can stabilize volatile compound development in cv. Sonsation across the harvest period, while natural light, especially at higher temperatures, can cause greater variability in aroma composition.

In conclusion, the results show that strawberry quality in cv. Sonsation is shaped by interacting effects of ripening temperature and light conditions, reflecting a clear balance between yield-related traits and aroma composition. Higher ripening temperatures enhanced the formation of esters and terpenoids associated with desirable aroma, but at the same time, resulted in a lower °Brix/acidity ratio, reduced fruit yield, and smaller fruit, traits that may negatively affect perceived sweetness and overall quality. In contrast, lower temperatures produced larger fruits and higher yields with a more favorable °Brix/acidity ratio, yet they were associated with a less complex volatile composition and an increased proportion of volatile compounds linked to off-flavor formation, such as acids and ketones. Light conditions during fruit ripening proved to play a significant role, as high-intensity light with continuous photoperiod enhanced sugar accumulation, improved the °Brix/acidity ratio, and increased the volatile content, particularly esters linked to floral and fruity aromas. Moreover, fruit ripened under continuous light conditions showed more stable volatile content across the harvests, while fruits under natural light had greater temporal variability, especially combined with higher temperatures. Together, these findings emphasize the importance of temperature and light and suggest relatively low temperatures (9–15 °C) along with a high daily light integral to support favorable yield and taste and aroma characteristics in cv. Sonsation.

To our knowledge, this study represents the first systematic investigation of how temperature and light regimes influence flavor-related chemical traits, including volatile composition, of cv. Sonsation fruit. By integrating yield parameters, sugar–acid balance, and volatile composition under well-controlled environmental conditions, the results extend previous studies that relied on limited environmental control or single-factor approaches and provide new insight into the mechanisms underlying flavor formation in strawberry. In the context of climate change and increasing use of controlled and semi-controlled production systems, these findings provide a practical basis for optimizing ripening conditions.

■ ASSOCIATED CONTENT

Supporting Information

The Supporting Information is available free of charge at <https://pubs.acs.org/doi/10.1021/acsagstech.5c01080>.

Multivariate statistical analyses (PCA and PLS-DA) of the volatile composition of cv. Sonsation fruit under experimental treatments (Figures S1–S5), detected volatile compounds (Table S1), and VIP scores for different experimental treatments (Tables S5–S7) ([DOCX](#))

Normalized peak areas of volatile compounds detected by HS-SPME-GC-MS in cv. Sonsation fruit (Tables S2–S4) ([XLSX](#))

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Notes

The authors declare no competing financial interest.

■ ACKNOWLEDGMENTS

This work was conducted as part of the project "TastyStrawberry", funded by the Norwegian Agricultural Agreement Research Fund/Foundation for Research Levy on Agricultural Products, grant number 336302, and Grofondet, grant number 210048.

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