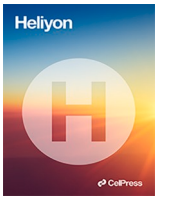
Heliyon 11 (2025) e41549

Contents lists available at ScienceDirect

Heliyon

journal homepage: www.cell.com/heliyon



Research article

Strawberry plant growth enhancement: Effects of artificial light and methyl jasmonate-salicylic acid treatments on physiology and metabolism

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ARTICLE INFO

Keywords:
Light emitting diode
Minor hormones
GC-MS and LC-MS
Lowland strawberries

ABSTRACT

Strawberries, known for their antioxidant properties, exhibit changes in physiology and metabolite profiles based on cultivation techniques. In Indonesia, strawberries are typically grown in highland regions, but climate change has necessitated adjustments in cultivation practices to enhance production and quality. This study investigates the adaptation of strawberry plants in lowland environments using light-emitting diodes (LEDs) and the exogenous application of methyl jasmonate (MeJA) and methyl salicylic acid (MeSA). A randomized block design was used with two factors: LED light types and MeJA–MeSA treatments. While the treatments did not significantly affect shoot growth (initially 1.5–2 cm, increasing 3–5 times by day 3), chlorophyll content, or fruit sugar levels, notable effects were observed in leaf glucose accumulation. The control group showed a fivefold increase (0.55 μg ml^{-1}), while LED-hormone treatments resulted in a 27–64 % lower increase (0.20–0.40 μg ml^{-1}). Fructose levels followed a similar pattern, and malic acid content was highest in the MeJA treatment (5.76 mg ml^{-1}), with MeSA treatments also enhancing malic acid (5.91 mg ml^{-1}). The secondary metabolite analysis, conducted using GC-MS and LC-MS, identified key defense-related compounds, including terpenoids, saturated fats, alkaloids, and amino acid derivatives, which play a role in the plant's defense mechanisms. These findings highlight the potential of LED lighting and hormone applications to modulate strawberry physiology and suggest further research into their role in plant stress responses.

1. Introduction

Owing to its exceptional organoleptic attributes and rich content of essential nutrients, vitamins, and minerals, strawberry (Fragaria × ananassa Duch.) remains a globally cherished fruit [1,2]. Strawberry plants are usually cultivated in the tropics in high-land areas, with elevations exceeding 1000 m above sea level and temperatures of 17°C-20 °C, as these conditions are favorable [3]. However, climate change and global warming have resulted in altered environmental conditions for highland plants, especially strawberries, thereby raising concerns about the extinction of this plant. Therefore, simple modifications in developing strawberry cultivation techniques are necessary for increased fruits production and quality and easy cultivation in all regions, especially in lowland areas. Applying artificial light and certain hormones can serve as simple environmental modifications for developing optimal

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https://doi.org/10.1016/j.heliyon.2024.e41549
Received 26 August 2024; Received in revised form 25 December 2024; Accepted 27 December 2024
Available online 30 December 2024

strawberry cultivation techniques.

Using artificial light in cultivation techniques can shorten the cycle of one-year crops, such as peas and canola [4]. Using a light-emitting-diode (LED) as artificial light in cultivating strawberry plants can modify plant metabolic pathways by accumulating photosynthate in sinks and regulating photosynthate flow. Carbohydrate translocation can also be optimized without interference from other sink competitors to achieve increased fruit yield and quality [5]. LEDs are solid-state lights and are durable. Their application can considerably improve plant growth, quality, and productivity. For instance, in strawberry cultivation, using red and blue LEDs in a 1:9 ratio enhances the quantity and length of flower stalks [6]. Moreover, LEDs in strawberries have been associated with an increased anthocyanin content compared with the control group [7]. In the case of blueberries, LED usage has reduced the juvenile period when applied for 12-h, followed by a transition to an 8-h period [8].

Hormone treatments can contribute to plant growth and development by regulating various physiological processes, including the induction and adaptation of plant defenses [9]. Salicylic acid and its derivatives, methyl salicylate (MeSA), can activate plant defense against biotrophic pathogens. Methyl salicylate (MeSA), a volatile organic compound, is synthesized from salicylic acid via a signal transduction pathway to trigger plant defense responses. Together with methyl jasmonate, they constitute endogenous signaling molecules that play a pivotal role in managing stress responses and plant development [10]. Jasmonic acid (JA) and its plant hormone derivative, methyl jasmonate (MeJA), participate in various physiological processes, particularly in modulating plant defense responses, including antioxidant capacity against pathogens and abiotic stress [11]. Both also considerably contribute to fruit growth and ripening regu-lation [12]. MeJA, a cyclopentanone-based compound derived from linolenic acid, is recognized as a crucial plant hormone owing to its ability to mediate intra- and inter-plant communication, facilitated by its capacity to diffuse through biological membranes and its volatile nature [13].

The exogenous application of the active form of jasmonic acid, methyl jasmonic (MeJA), can increase plant resistance to herbivorous insect pests by inducing plant defenses [14]. In strawberries, preharvest and postharvest applications of this acid resulted in accelerated fruit ripening and changes in the level of primary (e.g., sugars) and secondary metabolites (e.g., anthocyanins and polyphenols), resulting in enhanced fruit quality and shelf life [15–18]. Notably, while jasmonic acid has been linked to the activation of defenses against pests, necrotrophic pathogens, and nematodes [19,20], salicylic acid has been linked to the activation of defenses against biotrophic pathogens [10].

The use of artificial light and hormonal treatments is a well-established method for optimizing plant growth and influencing physiological responses. However, studies focusing on the application of these strategies to improve strawberry cultivation in Indonesia's lowland regions are still limited. By integrating physiological and metabolomic analyses, this study aims to uncover the mechanisms behind strawberry adaptation to artificial light and MeSA–MeJA treatments in lowland conditions. This approach is expected to enhance both the productivity and quality of strawberries grown in these environments.

2. Materials and methods

2.1. Planting and treatment applications

Planting was conducted at the screen house Leuwikopo Experimental Field, Department of Agronomy and Horticulture, IPB University. We obtained "California variety" seedlings from a strawberry nursery in Lembang, West Bandung Regency, West Java. LED lights were installed in a specific arrangement to facilitate the experimental treatments, as illustrated in Fig. 1a-d. The LED specifications include Fultrum LED Grow Lights (peak purple spectrum at 650 nm and a power consumption of 24 W). The arrangement was tailored to achieve a specific blue-to-red light ratio, which was further adjusted using additional LED strips. The Methyl Jasmonate (MeJA) and Methyl Salicylate (MeSA) utilized in this study were 95 % pure and procured from Sigma-Aldrich.

The experiment was conducted using a two-factor nested randomized complete block design (RCBD). Three experimental blocks

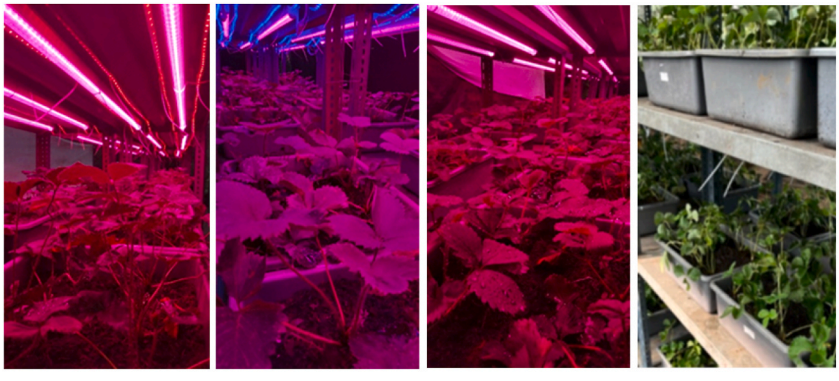

Fig. 1. The appearance of strawberry plants under LED treatments: (a) RB 2:1, (b) RB 1:2, (c) RB 1:1, and (d) control.

served as replications, with each treatment within a block consisting of eight plant samples, resulting in a total of 24 plants per treatment level. The first factor investigated the effects of different LED light combinations: Red (R) at a 2:1 ratio (RB 2:1), Blue (B) at a 1:2 ratio (RB 1:2), and a control with equal ratios (RB 1:1). The second factor involved the weekly application of MeSA and MeJA hormones, with each hormone tested at four concentrations: MeSA (0 mM, 2.5 mM, 5 mM, and 15 mM) and MeJA (0 mM, 2.5 mM, 5 mM, and 15 mM), in addition to a control level.

Strawberries were cultivated in trays measuring 40 cm × 30 cm × 13 cm, utilizing a substrate composed of soil and roasted husks. Irrigation was conducted every two days, delivering 100 ml of water per plant. Weekly fertilization was performed at a concentration of 1 gl^{-1}, accompanied by regular maintenance activities, including leaf pruning and manual control of plant pests.

2.2. Setting general conditions

Artificial lighting was applied for 20 h daily. Light intensity, measured with a LI-COR-1500 quantum sensor (μmol m^{-2} s^{-1}) at 15–20 cm above the plant canopy, revealed that LED B (Blue) peaked at 90 μmol m^{-2} s^{-1} at 12:00, while LED C (Red/Blue) and LED R (Red) peaked at 70 and 60 μmol m^{-2} s^{-1}, respectively (Fig. 2a). Humidity and temperature were monitored every 10 min using a digital thermometer (data logger) over a 2-month period. The average daily relative humidity (RH) in the greenhouse was 78.2 %, with a peak of 95.3 % in the morning and a minimum of 36.8 % during the day (Fig. 2b). The average temperature was 27.7 °C, with highs of 38.4 °C and lows of 20.8 °C (Fig. 2c).

2.3. Morphological observations

Morphological observations included shoot growth and the appearance of flowers and fruits. The speed of shoot growth was measured at a 3-day interval: 0, 3, 6, and 9 days. A total of 3 biological replicates were employed, with five technical replicates conducted for each treatment level.

2.4. Analysis of leaf chlorophyll, glucose, and fructose

The chlorophyll content in the leaves was tested in Weeks 2, 4, 6, and 8 after treatment using the spectrophotometric method [21]. Three biological replicates were used, with five technical replicates for each treatment level. Leaf samples were collected and pulverized with absolute methanol using a mortar. They were then centrifuged for 2 min at a speed of 16,873×*g*. The resulting supernatant was transferred, 200 μl at a time, into a 96-well flat-bottom polystyrene plate, and the absorbance values were measured at wavelengths of 652 and 665 nm. The chlorophyll *a* and *b* values were calculated using the following formula:

$$\text{Chla} = (-8.0962 \times \text{A6521cm}) + (16.5196 \times \text{A6651cm})$$

$$\text{Chlb} = (27.4405 \times \text{A6521cm}) - (12.1688 \times \text{A6651cm})$$

A652, 1 cm: Correction value for pathlength at 652.1 cm.
A665, 1 cm: Correction value for pathlength at 665.1 cm.

The glucose and fructose levels in the leaves were analyzed during Weeks 2, 4, 6, and 8 posttreatments. The analysis was performed using a spectrophotometric method, adhering to the procedure detailed in the Megazyme kit [22,23]. The Megazyme kit used was K-FRGLQR (D-Fructose/D-Glucose Assay Kit), and the calculation formulas were as follows:

$$\text{D-Glucose} = \text{A2} - (\text{A1} \times 203/223)$$

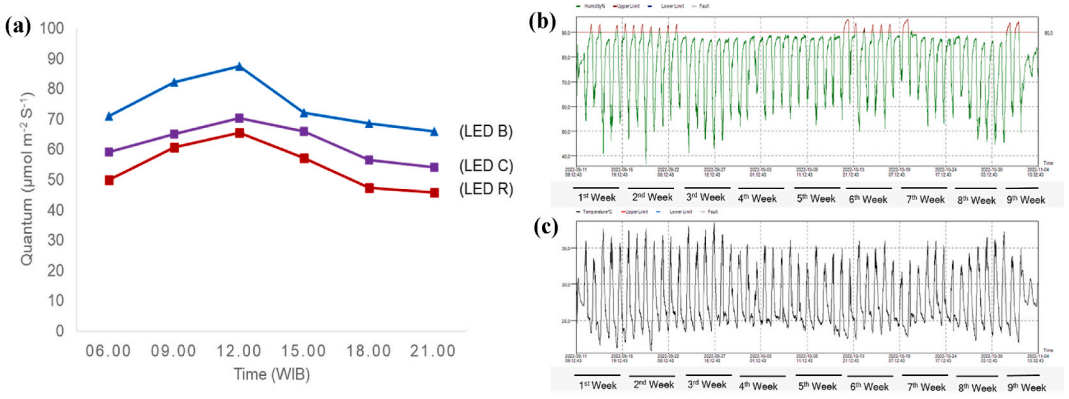

Fig. 2. Light intensity and environmental Conditions during artificial lighting treatment: (a) LED spectrums, (b) humidity, and (c) temperature monitoring.

D-Fructose = A3 − (A2 × 223/243)

A1–A3 are absorbance values at a wavelength of 340 nm.

2.5. Analysis of total dissolved solids (TDS) and total titrated acid (TTA), levels of glucose, fructose, and fruit organic acids

Fruit juice was extracted using a hand juicer for TDS testing (°Brix). Three biological replicates were used for each treatment level, with five technical replicates per level. The juice yield without adding water was measured using an Atago PAL-BX brix-acidity meter (300 μl) and a micropipette. For TTA testing (%), the juice was diluted with dis-tilled water at a ratio of 1:100 and then measured using an Atago PAL-BX brix-acidity meter (800 μl).

Furthermore, the content of glucose, fructose, and organic acids (malic, tartar, and citric) in the fruit was determined using the K-FRGLQR (D-Fructose/D-Glucose Megazyme Assay Kit), K-TART (Tataric Acid Megazyme Assay Kit), K-CITR (Citric Acid Megazyme Assay Kit), and K-Malc (Malic Acid Megazyme Assay Kits). The analysis was performed using the spectrophotometric method, following the procedure outlined in the relevant kit [24–26].

2.6. Secondary metabolite analysis (GC-MS and LC-MS)

The extraction method for GC-MS follows Halim et al. [27], while the extraction method for LC-MS is based on Song et al. [28]. Each analyzed sample is a composite of 3 replicates to reduce individual variability. Generally, the extraction methods are similar: 1 g of leaf powder is dissolved in 70 % methanol. Subsequently, sonication is per-formed at different times and temperatures: GC-MS for 60 min at 60 °C and LC-MS for 30 min at 28 °C. The extracts are injected into the Agilent Technologies 7890A/G3440A 5975C Inert/G3171A for GC-MS and UHPLC-Q-Orbitrap HRMS for LC-MS. The raw data obtained were then analyzed using the *Compound software Discover* 3.1 and *KnowItAll Informatic System* 2023 to identify the resulting metabolite compounds. The GC-MS and LC-MS analysis data were validated and cleaned to ensure their quality and accuracy. Compound identification was performed using the ChEBI database (https://www.ebi.ac.uk/chebi/), PubChem database (https://pubchem.ncbi.nlm.nih.gov/), and ChemSpider database (https://www.chemspider.com/). The KEGG Pathway Database analyzed the classification and function of several compounds in leaves subjected to MeJA and MeSA appli-cations (https://www.genome.jp/kegg/).

Fig. 3. The difference in plant conditions between those subjected to hormone treatment and those without treatment.

2.7. Analysis of nutrient status in leaves

The samples used were leaves that were 8 MSP (week after treatment). After oven-drying 80 g of leaves, they were crushed using a mortar and then sent to the Testing Laboratory, Department of Agronomy and Horticulture IPB. Three distinct methods were used for nutrient content testing: the trimetric method for N content, the spectrophotometric method for P content, and the atomic absorption spectrophotometry (AAS) method for K content and other micronutrients.

2.8. Data analysis

The collected data was analyzed using analysis of variance (ANOVA) at a 5 % significance level to evaluate the treatment effects. Duncan's Multiple Range Test (DMRT) was performed if the test results indicated significant effects. Data was analyzed using SAS software (SAS On Demand for Academics Version). In addition, secondary metabolite analysis was performed using the R Studio software (version 4.1.2) with several packages such as glots, cluster, and heatmap2.

3. Results

3.1. General plant conditions

A noteworthy observation in the context of plant growth conditions was the occurrence of pest attacks on the plants. A clear difference was observed when comparing plants treated with MeJA and MeSA hormones to untreated plants. The treated plants appeared healthy and showed few signs of pest infestation, such as aphids (Fig. 3). This observation highlights the potential role of hormone induction, specifically from the jasmonate and salicylate groups, in strengthening plant defense mechanisms against various stresses, including biotic factors such as pest and disease attacks. This finding is consistent with previous research efforts investigating the effects of hormone induction on plant resilience.

The application of LED light and MeJA-MeSA treatments induced generative reproductive organs earlier than vegetative propagation organs. In this study, stolon development occurred after the formation of flowers and fruits, approximately 5–6 weeks post-treatment. Although stolons formed under all treatment conditions, their numbers were minimal, averaging 1-2 stolons per plant. This may be attributed to the fact that stolon development followed the flowering and fruiting phases in strawberries, likely limiting stolon formation as photosynthetic assimilates were directed towards the development of flowers and fruits during the generative phase.

Flower emergence was observed around the third to fourth week following treatment, with fruit development occurring one week after full bloom and successful pollination. Pollination was conducted manually using a brush, as no pollinating insects were present in the screenhouse environment. Flowers and fruits were produced under all LED treatments, yet flowering induction did not occur in the control and high concentration jasmonate treatments, particularly at a concentration of 15 mM MeJA. This phenomenon is possibly related to the exogenous application of MeJA, which may suppress photosynthetic processes, thereby restricting assimilate availability to the vegetative phase alone.

3.2. Growth and development of shoots

Changes in shoot height were measured using a ruler at a 3-day interval from the beginning of emergence until the leaf buds fully

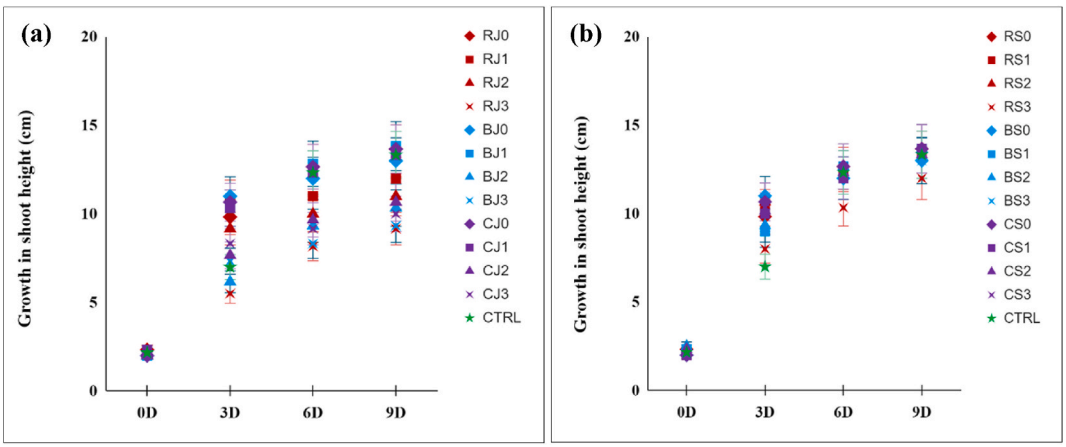

Fig. 4. Growth measurement of shoot height in different time intervals during treatment (a) LED + MeJA and (b) LED + MeSA.
*Notes: R = LED RB 2:1; B = LED RB 1:2; C = LED RB 1:1; J0 = MeJA 0 mM; J1 = MeJA 2.5 mM; J2 = MeJA 5 mM; J3 = MeJA 15 mM; S0 = MeSA 0 mM; S1 = MeSA 2.5 mM; S2 = MeSA 5 mM; S3 = MeSA 15 mM; CTRL = Control.

bloom (in strawberries, it occurs on day 9). New shoots on strawberries usually have a height of 1.5–2 cm. Changes in shoots continue to occur until the shoots fully bloom into full leaves, followed by elongation of the petioles, which can be interpreted as the plant height of the strawberry plant during growth. Strawberry plants usually experience a significant change in shoot height on day three after shoot appearance. In this study, the treatments did not have a statistically significant effect on plant height changes. However, the graph indicates that height increased 3–5 times from the initial height by day 3 (Fig. 4a and b).

3.3. Chlorophyll, glucose, and fructose levels of leaves

Chlorophyll in strawberry leaves was observed throughout the plant growth period from the second week after treatment until the eighth week. The levels of chlorophyll *a* and *b* in the leaves showed a decreasing trend in all treatments, both in the LED + MeJA and LED + MeSA treatments (Fig. 5a–d). The light intensity produced by the three LED treatments in this study appeared to have a small PPFD difference, showing that the light produced relatively does not affect chlorophyll accumulation in the leaves. Meanwhile, MeJA and MeSA did not significantly affect chlorophyll accumulation.

The levels of glucose in leaves showed a distinct response to the LED treatments combined with MeJA and MeSA (Fig. 6a and b). The control treatment led to a fivefold increase in glucose levels, reaching around 0.55 μg ml^{-1} by week eight. In contrast, LED and hormone treatments resulted in only about a threefold increase, reaching between 0.20 μg ml^{-1} and 0.40 μg ml^{-1}. This represents a 27 %–64 % lower glucose accumulation in the LED and hormone treatments compared to the control. On average, glucose levels in the control were about 45 % higher than those in the LED-hormone treatments.

Fructose levels exhibited a similar pattern (Fig. 6c and d), with the control treatment showing an approximate sevenfold increase, reaching around 0.60 μg ml^{-1} by the eighth week. In contrast, LED and hormone treatments resulted in a more modest increase, with fructose levels rising by about fourfold, peaking at approximately 0.20 μg ml^{-1} to 0.40 μg ml^{-1}. In the control group, fructose levels consistently surpassed glucose levels (>0.60 μg ml^{-1} vs. < 0.60 μg ml^{-1}), indicating a greater accumulation of fructose. However, in

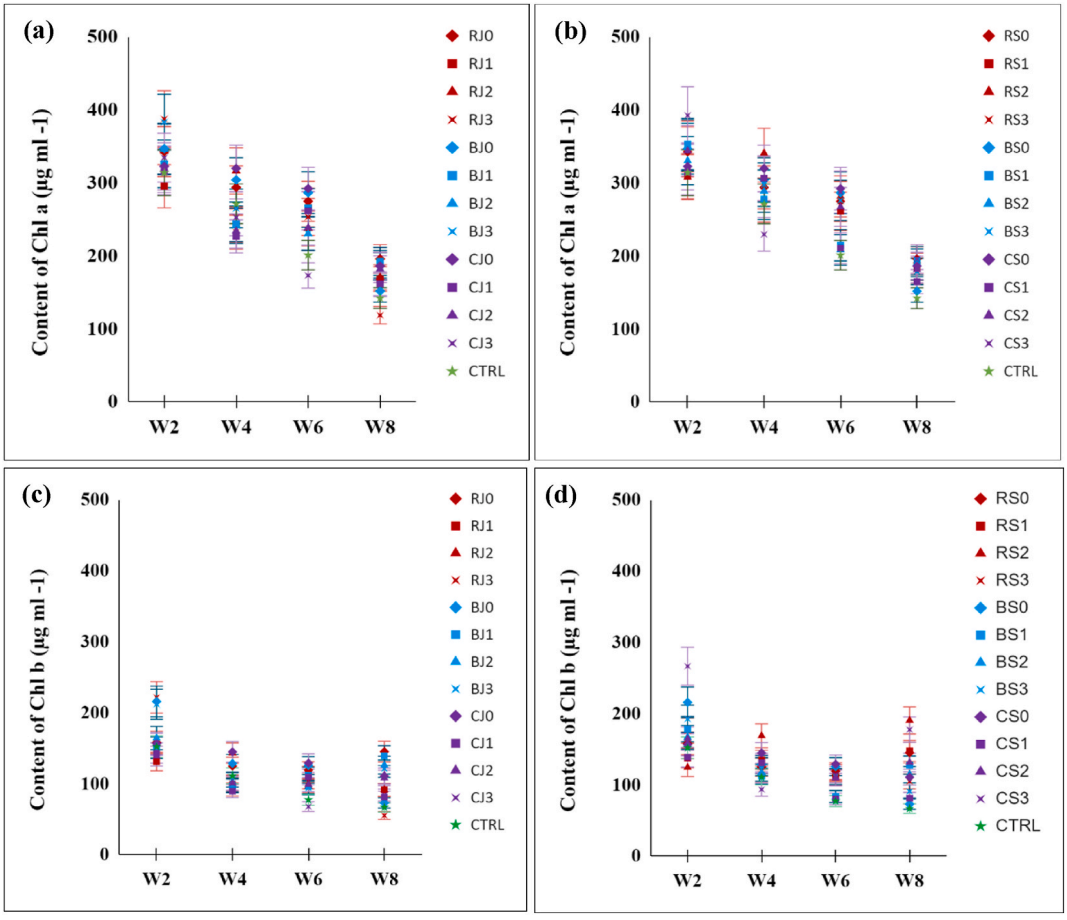

Fig. 5. Leaf chlorophyll *a* concentration under (a) LED + MeJA and (b) LED + MeSA, and leaf chlorophyll *b* concentrations under (c) LED + MeJA and (d) LED + MeSA.
*Notes: R = LED RB 2:1; B = LED RB 1:2; C = LED RB 1:1; J0 = MeJA 0 mM; J1 = MeJA 2.5 mM; J2 = MeJA 5 mM; J3 = MeJA 15 mM; S0 = MeSA 0 mM; S1 = MeSA 2.5 mM; S2 = MeSA 5 mM; S3 = MeSA 15 mM; CTRL = Control.

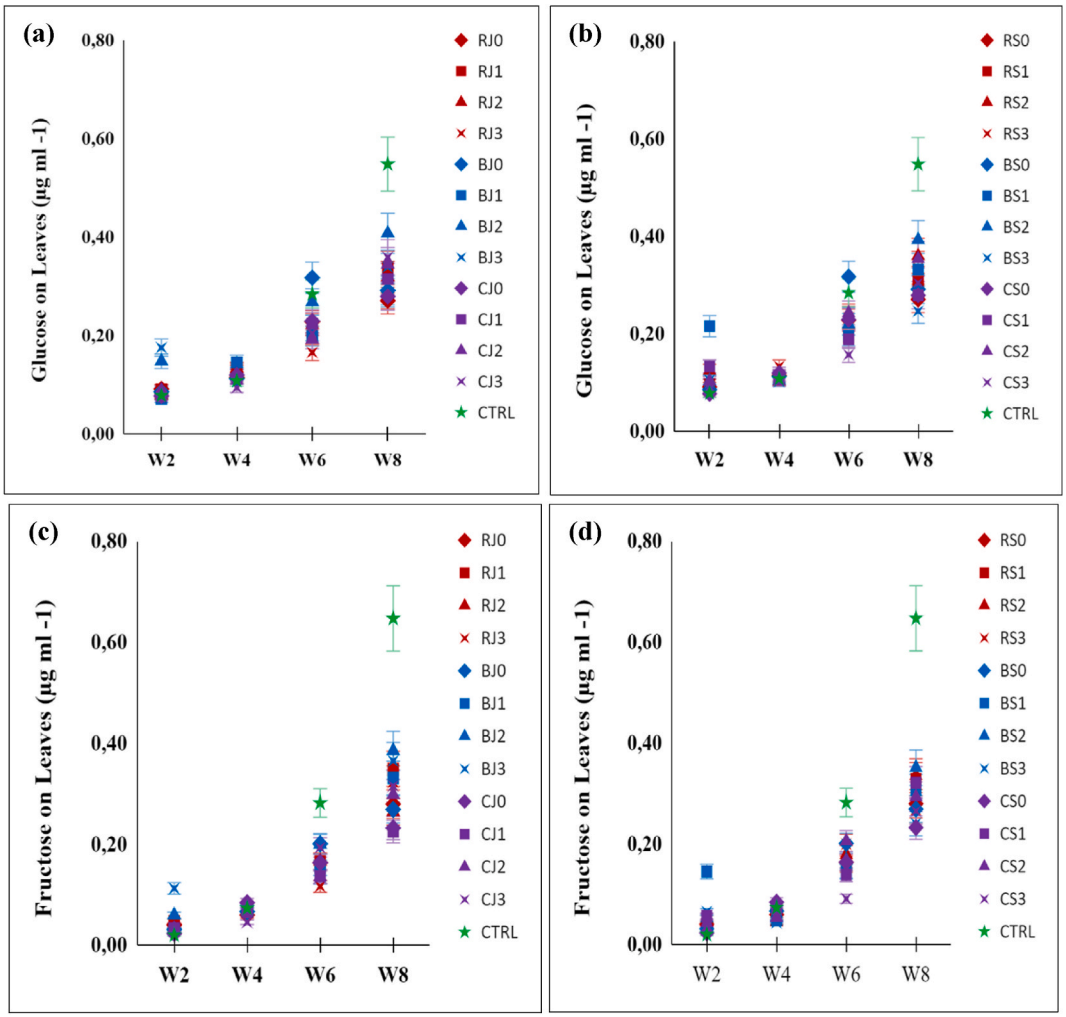

Fig. 6. Leaf glucose concentrations under (a) LED + MeJA and (b) LED + MeSA, and leaf fructose concentrations under (c) LED + MeJA and (d) LED + MeSA.
*Notes: R = LED RB 2:1; B = LED RB 1:2; C = LED RB 1:1; J0 = MeJA 0 mM; J1 = MeJA 2.5 mM; J2 = MeJA 5 mM; J3 = MeJA 15 mM; S0 = MeSA 0 mM; S1 = MeSA 2.5 mM; S2 = MeSA 5 mM; S3 = MeSA 15 mM; CTRL = Control.

the LED and hormone treatments, glucose and fructose levels remained relatively comparable, suggesting that these treatments may normalize the accumulation of both sugars. Overall, this indicates a modulatory effect of LED-hormone treatments, which seem to suppress and balance sugar levels in comparison to the control.

3.4. Total dissolved solids (TDS) and total titrated acid (TTA) levels of glucose, fructose, and fruit organic acids

TDS and TTA are the crucial chemical properties of fruits that affect their quality. TDS indicates the value of fruit sweetness, while TTA indicates the value of fruit acidity. The TDS and TTA values across all treatments with MeJA and MeSA showed no statistically significant differences. Both MeJA and MeSA treatments resulted in similar sweetness (TDS around 8–9 °Brix) and acidity levels (TTA between 2.5% and 3%) across concentrations, indicating that these treatments did not significantly alter the fruit's chemical composition.

In treatments with MeJA, low concentrations (0 and 2.5 mM) allowed for fruiting, but higher concentrations (5 and 15 mM) inhibited flowering and fruiting, especially under certain LED light conditions. This inhibition may be because of exogenous MeJA on photosynthesis, which can reduce the availability of assimilates necessary for reproductive [29,30]. Conversely, all MeSA treatments, even at 15 mM, produced fruit, suggesting that MeSA may be a more favorable treatment for fruit-bearing under LED lighting, as it maintains statistically similar TDS and TTA levels without negatively affecting reproductive growth (see Table 1).

The data presented in Tables 2a and 2b illustrate the effects of varying LED red-blue ratios combined with either MeJA or MeSA on the metabolite composition of strawberries. Glucose levels remained consistent across all treatments in both tables, ranging from 2.80

Table 1
TDS and TTA values in fruit as measured by *brix-acidity*.

Treatment	Methyl Jasmonate		Treatment	Methyl Salicylates	
	TDS	TTA		TDS	TTA
RJ0	9.47 ± 0.42 a	2.53 ± 0.14 a	RS0	9.47 ± 0.42 a	2.53 ± 0.14 a
RJ1	9.03 ± 0.52 a	3.73 ± 0.09 a	RS1	9.67 ± 0.41 a	3.12 ± 0.07 a
RJ2	–	–	RS2	8.13 ± 0.37 a	2.87 ± 0.13 a
RJ3	–	–	RS3	8.67 ± 0.17 a	2.98 ± 0.10 a
BJ0	8.40 ± 0.26 a	2.62 ± 0.06 a	BS0	8.40 ± 0.26 a	2.62 ± 0.06 a
BJ1	8.83 ± 0.50 a	2.79 ± 0.25 a	BS1	9.23 ± 0.20 a	3.15 ± 0.15 a
BJ2	8.70 ± 0.10 a	3.25 ± 0.30 a	BS2	9.40 ± 0.76 a	2.99 ± 0.05 a
BJ3	–	–	BS3	8.60 ± 0.25 a	3.01 ± 0.08 a
CJ0	8.73 ± 0.48 a	2.73 ± 0.03 a	CS0	8.73 ± 0.48 a	2.73 ± 0.03 a
CJ1	8.77 ± 0.20 a	3.22 ± 0.03 a	CS1	8.97 ± 0.32 a	2.83 ± 0.17 a
CJ2	8.52 ± 0.31 a	2.34 ± 0.20 a	CS2	9.40 ± 0.76 a	2.30 ± 0.03 a
CJ3	–	–	CS3	9.53 ± 0.74 a	2.34 ± 0.16 a
CTRL	–	–		–	–

Notes: Numbers followed by the same letter in the same column show not significantly different numbers based on Duncan's double test at the level of α = 5 %. R = LED RB 2:1; B = LED RB 1:2; C = LED RB 1:1; J0 = MeJA 0 mM; J1 = MeJA 2.5 mM; J2 = MeJA 5 mM; J3 = MeJA 15 mM; S0 = MeSA 0 mM; S1 = MeSA 2.5 mM; S2 = MeSA 5 mM; S3 = MeSA 15 mM; CTRL = Control; (−) = not subject to flowering.

Table 2a
Levels of glucose, fructose, and organic acids found in strawberries based on LED + MeJA treatment.

Treatment	Glucose (μg $^{ml-1}$)	Fructose (μg $^{ml-1}$)	Malic Acid (mg $^{ml-1}$)	Tartaric Acid (mg $^{ml-1}$)	Citric Acid (mg $^{ml-1}$)
RJ0	2.88 ± 0.02 a	0.31 ± 0.02 a	5.21 ± 0.04 ab	0.97 ± 0.28 a	0.19 ± 0.06 a
RJ1	2.88 ± 0.01 a	0.30 ± 0.01 a	3.77 ± 0.08 c	0.92 ± 0.09 a	0.31 ± 0.06 a
RJ2	–	–	–	–	–
RJ3	–	–	–	–	–
BJ0	2.86 ± 0.02 a	0.28 ± 0.01 a	4.40 ± 0.05 b	0.93 ± 0.29 a	0.21 ± 0.06 a
BJ1	2.78 ± 0.05 a	0.32 ± 0.05 a	4.85 ± 0.08 b	0.95 ± 0.15 a	0.22 ± 0.05 a
BJ2	2.83 ± 0.02 a	0.28 ± 0.01 a	4.41 ± 0.10 b	1.19 ± 0.20 a	0.32 ± 0.08 a
BJ3			–	–	–
CJ0	2.88 ± 0.01 a	0.31 ± 0.01 a	5.19 ± 0.09 ab	1.18 ± 0.34 a	0.18 ± 0.03 a
CJ1	2.87 ± 0.00 a	0.28 ± 0.00 a	5.76 ± 0.06 a	1.04 ± 0.26 a	0.14 ± 0.06 a
CJ2	2.80 ± 0.04 a	0.30 ± 0.02 a	5.02 ± 0.07 ab	1.03 ± 0.27 a	0.18 ± 0.02 a
CJ3	–	–	–	–	–
CTRL	–	–	–	–	–

Notes: Numbers followed by the same letter in the same column show not significantly different numbers based on Duncan's double test at the level of α = 5 %. R = LED RB 2:1; B = LED RB 1:2; C = LED RB 1:1; J0 = MeJA 0 mM; J1 = MeJA 2.5 mM; J2 = MeJA 5 mM; J3 = MeJA 15 mM; CTRL = Control; (−) = not subject to flowering.

Table 2b
Levels of glucose, fructose, and organic acids found in strawberries based on LED + MeSA treatment.

Treatment	Glucose (μg $^{ml-1}$)	Fructose (μg $^{ml-1}$)	Malic Acid (mg $^{ml-1}$)	Tartaric Acid (mg $^{ml-1}$)	Citric Acid (mg $^{ml-1}$)
RS0	2.88 ± 0.02 a	0.31 ± 0.02 ab	5.21 ± 0.04 ab	0.97 ± 0.28 a	0.19 ± 0.06 a
RS1	2.86 ± 0.02 a	0.27 ± 0.01 b	5.66 ± 0.08 ab	1.14 ± 0.19 a	0.16 ± 0.04 a
RS2	2.86 ± 0.03 a	0.33 ± 0.03 ab	4.45 ± 0.09 b	1.09 ± 0.15 a	0.28 ± 0.08 a
RS3	2.78 ± 0.04 a	0.35 ± 0.04 a	5.80 ± 0.09 ab	0.97 ± 0.18 a	0.35 ± 0.09 a
BS0	2.86 ± 0.02 a	0.28 ± 0.01 b	4.40 ± 0.05 b	0.93 ± 0.29 a	0.21 ± 0.06 a
BS1	2.84 ± 0.03 a	0.32 ± 0.04 ab	4.72 ± 0.10 b	1.15 ± 0.14 a	0.28 ± 0.04 a
BS2	2.85 ± 0.01 a	0.27 ± 0.00 b	5.80 ± 0.05 ab	0.86 ± 0.19 a	0.34 ± 0.08 a
BS3	2.79 ± 0.02 a	0.33 ± 0.03 ab	5.91 ± 0.06 a	0.84 ± 0.24 a	0.21 ± 0.05 a
CS0	2.88 ± 0.01 a	0.31 ± 0.01 ab	5.19 ± 0.09 ab	1.18 ± 0.34 a	0.18 ± 0.03 a
CS1	2.86 ± 0.04 a	0.34 ± 0.02 ab	5.04 ± 0.04 b	0.93 ± 0.25 a	0.24 ± 0.05 a
CS2	2.88 ± 0.02 a	0.27 ± 0.00 b	5.34 ± 0.09 ab	0.86 ± 0.26 a	0.33 ± 0.05 a
CS3	2.86 ± 0.03 a	0.28 ± 0.01 b	5.64 ± 0.04 ab	1.14 ± 0.24 a	0.13 ± 0.04 a
CTRL	–	–	–	–	–

Notes: Numbers followed by the same letter in the same column show not significantly different numbers based on Duncan's double test at the level of α = 5 %. R = LED RB 2:1; B = LED RB 1:2; C = LED RB 1:1; S0 = MeSA 0 mM; S1 = MeSA 2.5 mM; S2 = MeSA 5 mM; S3 = MeSA 15 mM; CTRL = Control.

to 2.88 μg ml^{-1}, showing no significant responsiveness to either treatment. Fructose levels varied more, particularly in the MeSA table, where treatments like RS3 showed a 12–29 % higher fructose content compared to the lowest treatment, suggesting that LED combined with MeSA may promote fructose synthesis more effectively than MeJA. This implies potential benefits for enhancing the sweetness of strawberries when using MeSA treatments.

Malic acid showed the most significant differences between the MeJA and MeSA treatments. The highest concentration was found in CJ1 (5.76 mg ml^{-1}) from the MeJA table, which was approximately 53 % higher than the lowest malic acid level in RJ1 (3.77 mg ml^{-1}). This highlights the stronger impact of MeJA combined with specific LED light ratios on malic acid synthesis. In the MeSA treatments, malic acid levels peaked at 5.91 mg ml^{-1} in BS3, indicating that MeSA can also enhance malic acid content, though to a slightly lesser extent compared to the highest MeJA treatment. Tartaric acid and citric acid remained relatively stable across both treatments, indicating minimal effect from either MeJA or MeSA combined with LED. These results align with existing literature, which indicates that jasmonate treatments can influence organic acid metabolism [29,31], while red light has been shown to impact fruit acid composition [32,33]. This suggests that the interaction between MeJA and LED lighting could modulate organic acid biosynthesis in strawberries, potentially affecting fruit quality traits like flavor and acidity.

Overall, the comparison shows that MeJA treatments are more effective at enhancing malic acid content, with CJ1 exhibiting the highest level, making it advantageous for improving fruit acidity and flavor. MeSA treatments, on the other hand, are more effective at boosting fructose levels, with RS3 showing a 29 % increase compared to the lowest treatment, potentially enhancing sweetness. Glucose and citric acid levels did not vary significantly between treatments, suggesting that neither treatment combination strongly influences these metabolites. These findings suggest that targeted use of MeJA or MeSA under specific LED conditions can selectively enhance key quality traits in strawberries, depending on the desired outcome.

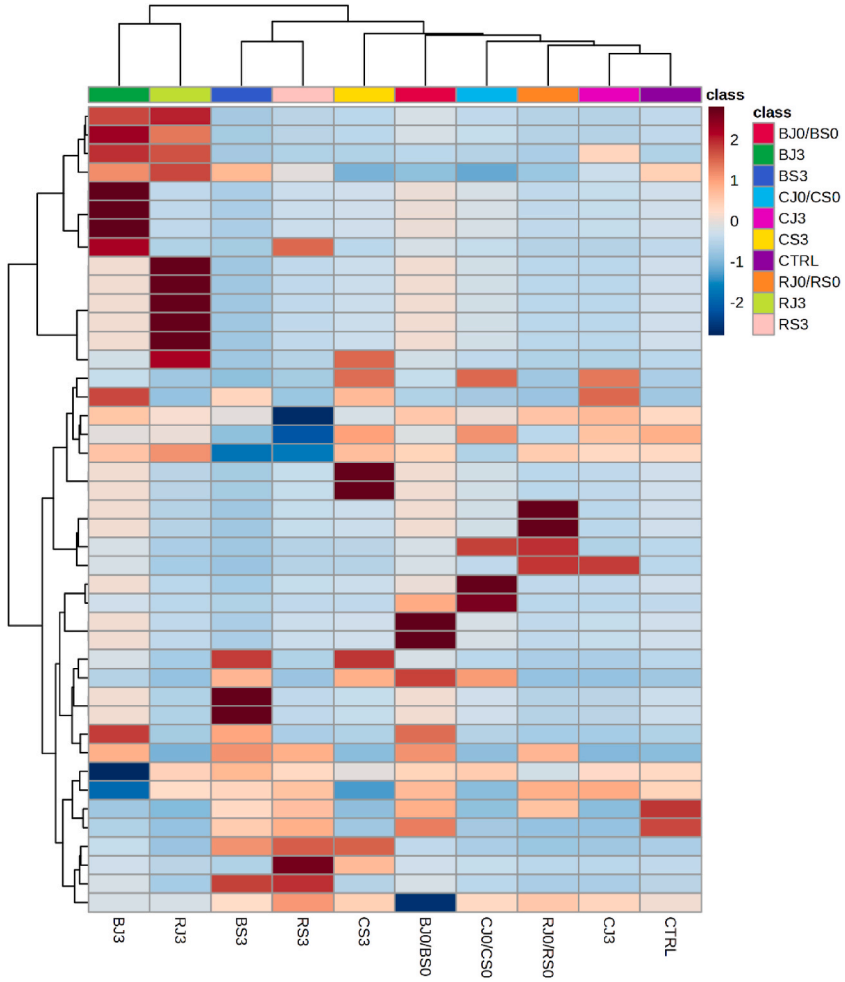

Fig. 7. Cluster analysis of the abundance of secondary metabolites of GC-MS results using heatmaps.
*Notes: R = LED RB 2:1; B = LED RB 1:2; C = LED RB 1:1; J0 = MeJA 0 mM; J3 = MeJA 15 mM; S0 = MeSA 0 mM; S3 = MeSA 15 mM; CTRL = Control.

3.5. Identification of secondary metabolites with GC-MS and LCMS

The heatmap in Fig. 7 illustrates the clustering of secondary metabolite abundances derived from GC-MS results, with samples grouped based on different combinations of LED light treatments (R and B, with varying red-to-blue ratios) and hormone treatments (MeJA and MeSA at 0 mM and 15 mM concentrations). The heatmap reveals that the primary factor influencing the clustering of secondary metabolite abundances is the type of hormone treatment (MeJA or MeSA) rather than the LED light ratios alone. Samples treated with the same hormone tend to group together, especially under specific LED light conditions (e.g., R or B lighting). For example, samples BJ3 and RJ3 (both treated with MeJA under different LED light ratios) cluster together, as do BS3 and RS3 (both treated with MeSA), indicating that the hormone type significantly impacts metabolite profiles, regardless of the LED spectrum. This effect is particularly strong under the R and B lighting conditions, where hormone-treated samples form distinct clusters according to the hormone used. In contrast, samples under LED C (with a 1:1 red-to-blue ratio) show clustering that is more like the control samples, suggesting that this balanced light ratio minimizes the impact of hormonal differences, leading to a more neutral metabolite profile. Overall, these patterns suggest that while LED light ratios do influence metabolite clustering, hormone treatments play a more dominant role, particularly under certain light conditions.

Based on the PCA analysis (Fig. 8a and b), the influence of the hormones MeJA and MeSA is more prominent in shaping the secondary metabolite profile compared to variations in LED light. In the hormone-based grouping, there is a clear separation between MeJA and MeSA treatments, indicating that each hormone significantly affects the accumulation of secondary metabolites. In contrast, in the light-based plot, samples exposed to different LED ratios appear clustered with overlapping distributions, suggesting that variations in red-blue light spectrum ratios do not produce significant differences in metabolite composition. These findings align with the roles of MeJA and MeSA as signaling molecules that specifically induce distinct secondary metabolite biosynthetic pathways,

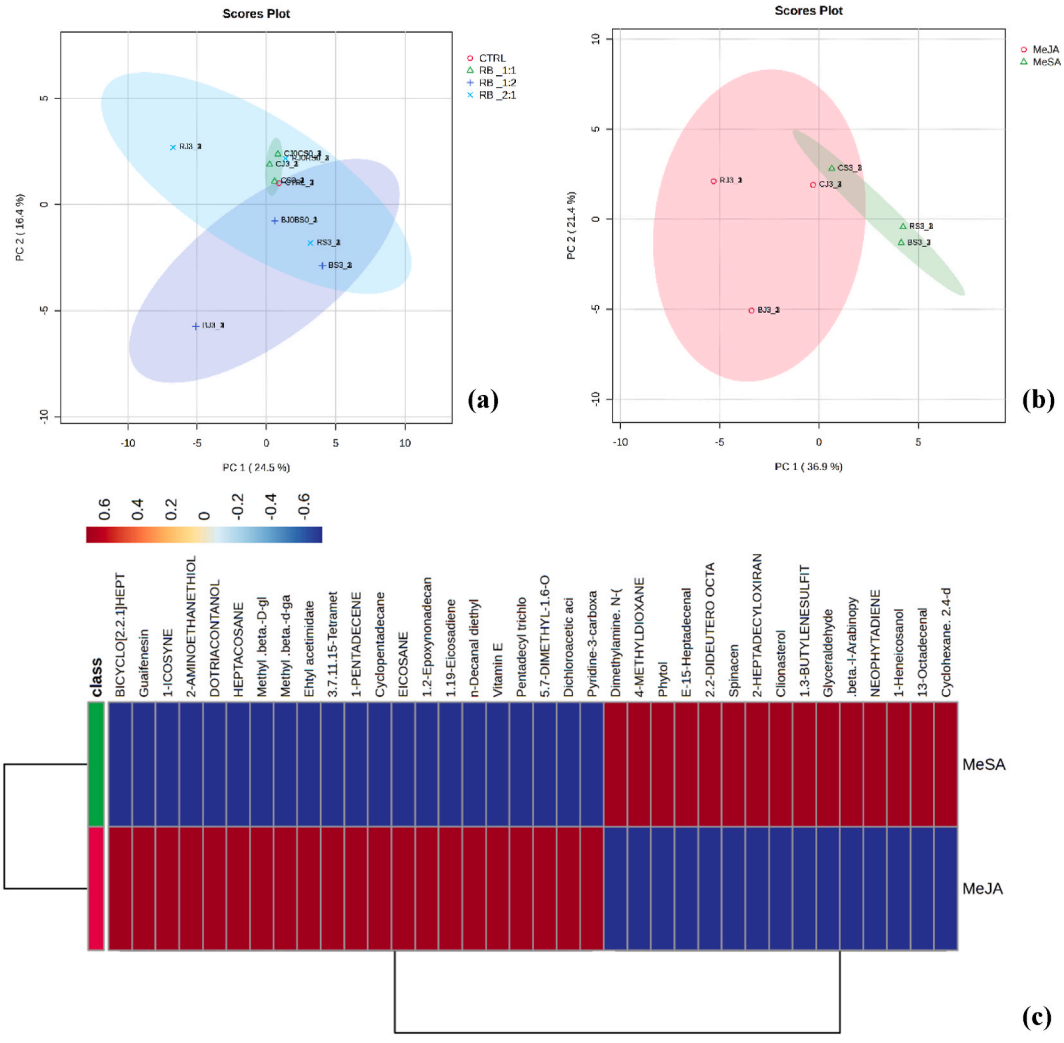

Fig. 8. Comparative effects of meja and mesa on secondary metabolite profiles versus led light variations: (a) PCA analysis of led treatments, (b) PCA analysis of hormone treatments, and (c) heatmap displaying metabolite expression abundance under hormonal treatments.

whereas the effect of LED light on secondary metabolism may require optimized intensities or spectral combinations to exert a more pronounced impact.

Based on the expression on heatmap analysis (Fig. 8c), the application of MeJA and MeSA results in distinct regulation patterns for secondary metabolites. Some compounds are upregulated in response to MeJA, while others show upregulation with MeSA, and similarly, each hormone also downregulates certain metabolites. This variation indicates that MeJA and MeSA differently modulate the levels of specific secondary metabolites in the plant.

Building on this analysis, an in-depth exploration of the biological roles of these specific compounds was conducted using the Kyoto Encyclopedia of Genes and Genomes (KEGG) database. The findings suggest these compounds can act as defense mechanisms against fungal, bacterial, and insect attacks (Table 3). This connection highlights that producing specific secondary metabolites, influenced by MeJA-MeSA hormone application, plays a crucial role in bolstering the plant's defense system against various biotic stressors. The number of compounds identified by LC-MS was relatively lower than that of GC-MS. This shows that the compounds contained in strawberry leaves are volatile and nonpolar. Some compounds were derived from amino acids, carotenoids, saturated fats, and terpenoids. The identified compounds were further analyzed in terms of their roles and functions in plant metabolism.

3.6. Plant nutrient status

The accumulation of NPK nutrients varied across treatments, with nitrogen (N) showing no significant differences (Fig. 9a). Phosphorus (P) accumulated most in the control and the 1:1 RB (red-blue) LED treatments (Fig. 9b), with MeSA-treated plants showing higher P levels than those treated with MeJA. In contrast, potassium (K) accumulation was highest in the 2:1 RB LED treatment, with both MeSA and MeJA enhancing K levels (Fig. 9c). The lowest calcium (Ca) accumulation occurred in the RB 1:1 without hormones and RB 2:1 with J3 treatment groups (Fig. 9d). Magnesium (Mg) content was highest in the control group compared to other treatments, including the 1:1 RB LED with MeSA and MeJA (Fig. 9e). Sodium (Na) accumulation was lowest in the control (Fig. 9f). Iron (Fe) content increased in the 1:1 RB LED treatment with both MeSA and MeJA (Fig. 9g), copper (Cu) was highest in the control (Fig. 9h), and zinc (Zn) levels peaked in the 1:1 RB LED treatment (Fig. 9i).

No distinct patterns or groupings were observed in the accumulation of macro and micronutrients as influenced by either the LED treatments or the MeJA and MeSA applications. This lack of clear trends may be attributed to the complex interactions between the light spectrum, hormonal treatments, and nutrient uptake mechanisms, which can vary based on the physiological and metabolic state of the plants under different conditions. Furthermore, other environmental factors or internal plant regulatory mechanisms could have influenced nutrient absorption, contributing to the inconsistent accumulation patterns observed across treatments.

4. Discussion

The role of jasmonates and salicylates in enhancing plant defenses against abiotic stresses has been well established through studies by Pieterse et al. [9], Yu et al. [14], War et al. [19], and Okada et al. [20]. These hormones activate a cascade of molecular defense responses, leading to improved resilience against environmental pressures. The reduction in pest infestation in hormone-treated plants supports this defense mechanism activation. However, contrary to some studies, high concentrations of jasmonates applied to plants like kanigara, soybean, and tomato resulted in significant height reductions [34], suggesting that while jasmonates can bolster defence, they may also suppress plant growth. Exogenous MeJA has been shown to reduce photosynthesis and inhibit growth [29], unlike salicylates, which tend to have a minimal effect on growth. This growth inhibition aligns with known effects of jasmonates, including root shortening and anthocyanin accumulation [11].

In addition to hormone treatments, LED light has been explored for its effects on plant growth. LEDs with a higher blue-light ratio generally promote more growth compared to those with a reduced red-light ratio, potentially due to the positive impact of blue light on cell elongation [32]. Consistent with these findings, blue LED light has been shown to significantly enhance petiole elongation in strawberry varieties "Daewang" and "Elsanta" [6,7,33]. However, exposure to blue LEDs over prolonged periods may reduce chlorophyll levels, likely due to the generative phase being triggered earlier [7,35]. Plant responses to light vary by species, and blue light typically induces less chlorophyll accumulation compared to red light in strawberries [7,33]. Similarly, the application of jasmonates has been associated with reduced chlorophyll levels and increased anthocyanin accumulation [29].

Carbohydrates, particularly glucose and fructose, are key indicators of photosynthetic activity. LED treatments that combine red and blue light have been shown to enhance glucose and fructose levels in strawberry leaves [36]. Red light specifically stimulates sugar accumulation [37], and jasmonate treatments further increase fructose content in plants [15]. The elevated glucose and fructose levels observed in this study may be linked to the acceleration of the generative period, during which plants demand more photosynthates to support flower and fruit formation [38].

Despite these effects on leaf nutrient accumulation and sugar metabolism, climatic conditions, cultivation practices, and plant genetics play a substantial role in influencing fruit quality parameters, such as total soluble solids (TDS) and titratable acidity (TTA) [39]. Studies have shown that LED light treatments had minimal impact on TDS and TTA values in strawberries [7,33]. Preharvest MeJA treatments, however, have been found to increase TTA without significantly affecting TDS [40,41], which is consistent with our findings that MeSA had no significant impact on TDS.

The interplay between jasmonates, photosynthesis, and nutrient accumulation may explain some of the observed effects. Exogenous MeJA can reduce photosynthetic activity in some species, thereby limiting the assimilates available for vegetative growth [29,30]. The lack of flowering observed in the control group without LED light exposure supports Wargent's [5] findings, which suggest that LED light enhances photosynthate translocation from source to sink, optimizing carbohydrate allocation during fruit filling.

Table 3
Results from KEGG classification and role in plants on various compounds in MeJA and MeSA treatments to contribute to plant defense mechanisms against biotic and abiotic stress.

No	Compound	Group	Chromatography Methods	Role in plants
1	β-linalool	Terpenoid	GC-MS	Metabolism of terpenoids and polyketides
2	Methyl β-L-arabino pyranoside	Terpenoid	GC-MS	Metabolism of terpenoids and polyketides
3	Phytol	Terpenoid	GC-MS	Synthesis of chlorophyll and tocopherol
4	Neophytadiene	Terpenoid	GC-MS	Antimicrobacterial agents (signaling and cellular processes)
5	Vitamin E	Terpenoid	GC-MS	Metabolism of co-factors and vitamins (Photoprotection)
6	Clionasterol	Terpenoid	GC-MS	Components of biological membranes (Phytosterol)
7	Squalene	Terpenoid	GC-MS	Components of biological membranes (Phytosterol)
8	Guaifenesin	Organooxygen	GC-MS	Metabolism of carbohydrate
9	Methyl β-D-galacto pyranoside	Organooxygen	GC-MS	Metabolism of carbohydrate
10	Glyceraldehyde	Organooxygen	GC-MS	Metabolism of carbohydrate
11	1,19-Eicosadiene	Fatty Acid	GC-MS	Anti-fungal agents (signaling and cellular processes)
12	Pentadecyl trichloro acetate	Fatty Acid	GC-MS	Stress and detoxification metabolism
13	Nonanal diethyl acetal	Fatty Acid	GC-MS	Flavor and fragrance agents
14	1-Heneicosanol	Fatty Acid	GC-MS	Hormone biosynthesis (mass trapping of insects using pheromones)
15	Cyclopentadecene	Fatty Acid	GC-MS	Hormone biosynthesis (mass trapping of insects using pheromones)
16	Eicosane	Fatty Acid	GC-MS	Anti-fungal agents (signaling and cellular processes)
17	3-Methylbutanoic acid	Fatty Acid	GC-MS	Flavor and fragrance agents
18	Morpholine	Alkaloid	GC-MS	Anti-fungal agents (signaling and cellular processes)
19	1,2-Epoxynonadecane	Alkaloid	GC-MS	Anti-fungal agents (signaling and cellular processes)
20	Pyr,3-carboxamide, oxime-N-(2-trifluoro Methyl phenyl)	Alkaloid	GC-MS	Anti-bacterial agents (signaling and cellular processes)
21	Phenylalanine	Phenylpropanoids	LC-MS	Immune system (stress conditions: drought, salinity, and insects)
22	9-cyanoantrachene	Phenanthrenes	LC-MS	Phytoanticipins (plant-insect interactions)
23	Astaxanthin	Carotenoids	LC-MS	Protects plants from photodamage
24	Octadecatrienoic Acid	Fatty Acid	LC-MS	Plant defense response to pathogenic infection
25	Toosendanin	Limonoids	LC-MS	Biopesticides
26	Phytofluene	Carotenoids	LC-MS	Photosynthesis and photoprotection
27	Vinyl Palmitate	Fatty Acid	LC-MS	Anti-bacterial
28	Isochiapin B	Sesquiterpenes	LC-MS	Anti-insect and anti-microbial

Jasmonate treatments have also been linked to shifts in organic acid metabolism [29,31], and red light can influence fruit acid composition [32,33], as evidenced by the high malic acid accumulation under blue light and salicylate application in this study. This observation confirms that blue light can impact organic acid synthesis and fruit accumulation [42].

The role of metabolites, such as phytol and neophytadine, in chlorophyll synthesis, photoprotection, and antimicrobial activity further underscores the complex interplay between light, hormones, and plant metabolism [43,44]. Compounds identified through LC-MS, like phenylalanine and 9-cyanoantrachene, are critical for plant defense against biotic and abiotic stresses [45,46]. Additionally, metabolites like toosendanin and isochiapin B are known for their roles in defense against bacteria and insects [47,48]. Jasmonate's influence on secondary metabolite biosynthesis, such as phytoalexins and alkaloids, further strengthens plant resistance against pathogens and insects [49].

Finally, the systemic acquired resistance (SAR) mechanism, regulated by salicylic acid and jasmonate, highlights the plant's ability to mobilize defense responses upon pathogenic attack [50,51]. The lack of studies on the combined effects of LED light and MeSA–MeJA treatments on nutrient accumulation in leaves leaves a gap in understanding. However, findings from lettuce studies provide some insights, where LED treatments led to variable effects on nutrient accumulation, such as increased calcium but decreased potassium, phosphorus, and magnesium [52–54]. This variability suggests that the interactions between LED light and hormone treatments may be species-specific, requiring further investigation to fully understand their combined impact on nutrient dynamics.

5. Conclusions

The combination of LED light treatment and exogenous application of methyl jasmonate (MeJA) and methyl salicylate (MeSA) affected strawberry physiology and metabolism in distinct ways. The MeJA treatment led to slower shoot growth compared to MeSA, but both treatments influenced sugar metabolism. While there was no significant change in total dissolved solids (TDS), total titratable acidity (TTA), glucose, citric acid, or tartaric acid levels in the fruits, fructose and malic acid showed differential accumulation. Specifically, MeJA and MeSA increased malic acid content significantly, suggesting a role in fruit quality enhancement. The analysis of secondary metabolites using GC-MS and LC-MS identified key compounds, including terpenoids, saturated fats, alkaloids, and amino acid derivatives, which are linked to the plant's defense mechanisms. These results indicate that the LED treatments, in conjunction with hormone applications, can influence the metabolic profile of strawberry plants, potentially improving their adaptive responses to

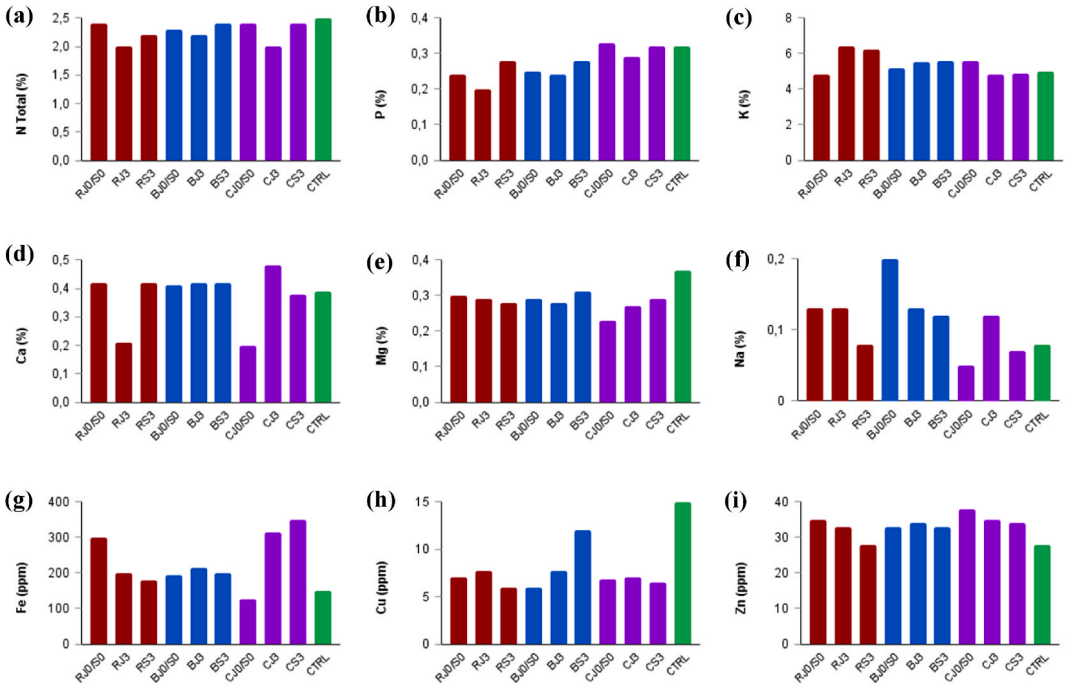

Fig. 9. Nutrient accumulation across LED and hormone treatments: (a) Nitrogen (N), (b) Phosphorus (P), (c) Potassium (K), (d) Calcium (Ca), (e) Magnesium (Mg), (f) Sodium (Na), (g) Iron (Fe), (h) Copper (Cu), and (i) Zinc (Zn).
Notes: R = LED RB 2:1; B = LED RB 1:2; C = LED RB 1:1; J0 = MeJA 0 mM; J3 = MeJA 15 mM; S0 = MeSA 0 mM; S3 = MeSA 15 mM; CTRL = Control.

environmental stress. However, further research is needed to fully understand the implications of these findings for strawberry cultivation in lowland regions.

CRediT authorship contribution statement

M. Adrian: Writing – original draft, Visualization, Software, Project administration, Investigation, Data curation, Conceptualization. **Roedhy Poerwanto:** Writing – review & editing, Validation, Supervision. **Eiichi Inoue:** Writing – review & editing, Validation, Supervision. **Deden Derajat Matra:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization.

Data availability statement

The data supporting this study are available upon request. To obtain the data, please contact the corresponding author.

Ethics approval

Review and/or approval by an ethics committee was not needed for this study because there was no human and animal participation involved.

Funding statement

This research was funded by The Ministry of Education, Culture, Research, and Technology (KEMENDIKBUDRISTEK), the Republic of Indonesia, the Fundamental Research Scheme of IPB University (PDUPT - Penelitian Dasar Unggulan Perguruan Tinggi) in 2022–2023 under the grant awarded to Deden Derajat Matra.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Deden Derajat Matra reports equipment, drugs, or supplies was provided by IPB University. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank the Indonesia Endowment Fund for Education (Lembaga Pengelola Dana Pendidikan, LPDP), Ministry of Finance of the Republic of Indonesia, for providing financial support for the education and academic studies of M Adrian.

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