

Article

Controlled Application of Far-Red Light to Improve Growth and Bioactive Compound Yield in *Centella asiatica*

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Abstract

This study examined how far-red (FR) light supplementation influences triterpene glycoside accumulation in *Centella asiatica* grown under different light intensities (50–200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) over 5 weeks. Four major compounds—madecassoside, asiaticoside, madecassic acid, and asiatic acid—were quantified. Results from three-way ANOVA showed that light intensity and time significantly affected the accumulation of all compounds, with FR light selectively enhancing glycoside levels but not triterpene acids. Although total glycoside content declined over time, plants under 200FR conditions retained the highest levels by week 5. Principal component analysis suggested that FR light modulates resource allocation between growth and secondary metabolism. These findings advance our understanding of light-mediated regulation in phytochemical biosynthesis and offer a basis for optimizing cultivation strategies in controlled environments. Notably, the compound-specific responses to FR suggest differential regulation within the triterpene biosynthetic pathway, opening avenues for targeted enhancement of medicinally important compounds.

Keywords: *Centella asiatica*; far-red light; plant factory; triterpene glycosides; secondary metabolites; light quality; phytochrome; madecassoside; asiaticoside



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1. Introduction

Centella asiatica (*C. asiatica*), a perennial herbaceous plant belonging to the Apiaceae family, is natively distributed in humid environments of tropical and subtropical regions, including India, Sri Lanka, and Africa [1]. This plant can propagate through both seeds (sexual reproduction) and stolons (asexual reproduction), with the latter being the preferred agricultural method where adventitious roots are induced from nodes [2]. *C. asiatica* has long been used as a medicinal plant in traditional Asian medicine, containing triterpene glycosides such as madecassoside, asiaticoside, madecassic acid, and asiatic acid as its main bioactive compounds [3]. These compounds exhibit various pharmacological activities, including skin regeneration, wound healing, anti-inflammatory, and antioxidant effects, leading to rapidly increasing demand in cosmetic and pharmaceutical industries [4]. In addition to its well-documented antioxidant activity, recent studies have demonstrated that *C. asiatica* exhibits antibacterial, anticancer, and neuroprotective properties through in vitro

and in vivo models [5,6]. These pharmacological properties contribute to its traditional use in managing inflammatory skin conditions such as eczema and psoriasis.

Plant growth and secondary metabolite biosynthesis are significantly influenced by the light environment. Light intensity and light quality are key regulatory factors in plant physiology and development [3]. Light intensity, measured as the number of photons incident on a unit area per unit time ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), directly affects photosynthetic efficiency and biomass production. Previous studies have reported that *C. asiatica* cultivated under high light intensity conditions showed increased fresh and dry weights, as well as enhanced content of the four triterpene glycosides [7]. Additionally, research has shown that increased shading leads to decreased asiaticoside and madecassoside content, confirming the importance of light intensity in the accumulation of bioactive compounds in *C. asiatica* [8].

Light quality plays a decisive role in plant morphogenesis, physiological responses, and metabolite accumulation by acting on various photoreceptors in plants [9]. Far-red light (700–800 nm) in particular regulates plant growth and development through the phytochrome signaling pathway involved in photomorphogenesis [10]. Phytochromes are reversible photoreceptors that convert to an active form (Pfr) under red light (660 nm) and revert to an inactive form (Pr) under far-red light [11]. The ratio of red to far-red light (R:FR) is a critical factor regulating plant morphogenesis and secondary metabolite biosynthesis. Low R:FR ratios (increased far-red light proportion) induce shade avoidance responses in plants, causing morphological changes such as stem elongation, leaf area expansion, and reduced branching, while also affecting secondary metabolite biosynthesis pathways [10].

Far-red light typically interacts with other wavelengths rather than acting independently, creating complex effects on plant physiology [11]. The supplemental effects of far-red light in environments with mixed red and blue light vary depending on plant species and cultivation conditions. In studies of plants containing triterpene compounds similar to those in *C. asiatica*, ginsenoside content in ginseng was significantly altered by the ratio of red to blue light (R:B) and far-red light (FR) treatment [12]. Similarly, gypenoside content was significantly higher under monochromatic red light and notably lower under blue and green light [13,14]. However, existing research on light environments for *C. asiatica* has primarily focused on light intensity and photoperiod, with a lack of systematic studies on the effects of far-red light on growth and functional metabolite accumulation [3,4,7,8]. Information on the complex effects of far-red light treatment on physiological responses and triterpene glycoside biosynthesis under various light intensity conditions is particularly limited [8].

Vertical farms are closed systems isolated from the external environment, representing advanced agricultural technology that enables a year-round stable crop production regardless of season or region by precisely controlling light, temperature, humidity, carbon dioxide concentration, and nutrients [15]. Artificial light plant factories can maintain optimally controlled growth conditions regardless of external environmental changes, allowing for planned production of high-quality crops [3]. Vertical farms are particularly suitable for producing high-value crops rich in functional compounds, as precise environmental control can maximize both biomass enhancement and secondary metabolite content. LEDs (Light-Emitting Diodes) have recently become the primary light source in plant factories due to their high energy efficiency, long lifespan, and ability to precisely generate various specific wavelengths [16,17]. LEDs can efficiently supply red (660 nm) and blue (450–470 nm) wavelengths critical for plant photosynthesis. Additionally, various wavelength LEDs, including green, yellow, and far-red, have been developed, enabling the creation of optimal light environments tailored to specific crops [8]. Far-red LEDs in particular are valued as

important tools for controlling plant growth and secondary metabolite biosynthesis by targeting phytochromes that play crucial roles in plant photomorphogenesis [10].

In Korea, various cosmetics and pharmaceuticals containing *C. asiatica*'s main components have been developed, with demand and consumption gradually increasing. However, domestic cultivation areas and yields of *C. asiatica* are very limited, causing most demand to be met through imports. In this context, establishing a year-round stable production system for *C. asiatica* using plant factories could play an important role in reducing import dependence and expanding domestic production. The use of far-red light in plant factory environments is gaining attention as a novel approach to controlling plant photomorphogenesis. Far-red light influences plant growth patterns, morphological development, and secondary metabolite biosynthesis through phytochrome photoreceptors. By adjusting the ratio of red to far-red light (R:FR), it is possible to alter plant resource allocation strategies and potentially enhance the biosynthesis of specific secondary metabolites. The biosynthesis of terpene compounds such as triterpene glycosides is known to be particularly sensitive to light environmental conditions, suggesting the potential for enhancing functional compound content in *C. asiatica* through far-red light treatment [18].

Therefore, the purpose of this study is to investigate the effects of various light intensity conditions and far-red light supplementation on the growth and triterpene glycoside accumulation of *C. asiatica* in a plant factory environment. This study is expected to contribute to enhancing the competitiveness of the domestic *C. asiatica* industry by establishing a stable year-round production system for high-quality plants enriched with bioactive compounds.

2. Materials and Methods

2.1. Plant Materials and Cultivation Conditions

This investigation utilized *Centella asiatica* L. Urban specimens sourced from a specialized medicinal herb nursery in Hapcheon, Korea. To establish experimental uniformity, stolon segments containing 3–4 fully expanded leaves were excised from mature stock plants and subjected to hydroponic root induction for seven days in deionized water. Following adventitious root development, the regenerated plantlets were transplanted into 128-cell horticulture plug trays containing a composite substrate (peat moss/vermiculite/perlite, 7:2:1 v/v/v) with pH 5.8–6.2.

The cultivation phase was conducted within environmentally regulated growth chambers integrated into a closed-type plant factory system (Model PF-3KE, Dasol Scientific, Hwaseong-si, Republic of Korea). Environmental parameters were programmed to maintain diurnal temperature fluctuations of 24/18 °C (day/night), with atmospheric moisture stabilized at $60 \pm 5\%$ relative humidity. Nutrient delivery employed a modified deep flow technique with recirculating solution formulated for leafy vegetables (N-P-K composition 13-5-7, electrical conductivity 1.2 dS/m, pH 5.8) replenished at 72 h intervals. Carbon dioxide concentration was monitored continuously (SenseAir CO₂ Engine, T&D Corporation, Nagano, Japan) and maintained at 400 ± 20 ppm throughout the experimental duration.

2.2. Far-Red Light Treatment and Experimental Design

The light treatment protocol incorporated a bifactorial design examining the interaction between photosynthetic photon flux density (PPFD) and spectral quality. Custom-fabricated illumination arrays utilizing precision light-emitting diodes delivered four distinct PPFD levels (50, 100, 150, and 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) across two spectral configurations. All treatments maintained a consistent red/blue ratio (R:B = 8:2) using monochromatic red (peak emission 660 ± 5 nm) and blue (peak emission 450 ± 5 nm) LEDs (Samsung Electronics, Jeonju-si, Republic of Korea). The experimental treatments included supplementary far-red radiation (peak emission 730 ± 5 nm) calibrated to establish a red/far-red

photon ratio (R:FR) of 1.0, while control treatments received equivalent photosynthetic photon flux without far-red augmentation. The photoperiodic regime employed a 14/10 h photoperiod/scotoperiod cycle for all treatments. Spectral distribution and photon flux density were measured at the plant canopy level using a calibrated spectroradiometer (SpectraPen LM 510, Photon Systems Instruments spol. s r.o., Drásov, Czech Republic) to verify both intensity and spectral uniformity across the cultivation area. The experimental architecture followed a completely randomized design with three replications per treatment combination and 12 plants per experimental unit. The cultivation cycle extended for five consecutive weeks, with systematic data collection at weekly intervals. Terminal harvest at week 5 provided comprehensive biomass data through destructive sampling of six randomly selected specimens per treatment.

2.3. Growth Measurements

Morphological development and growth metrics were systematically documented at weekly intervals (weeks 0–5) throughout the cultivation period. Non-destructive measurements included leaf proliferation index (total leaf count), dimensional parameters (leaf length, width, petiole elongation), root extension, stolon development (runner count), and leaf surface area. Leaf area determination utilized digital image acquisition followed by analytical processing with ImageJ software version 1.53t (National Institutes of Health, Bethesda, MD, USA), incorporating calibrated pixel-to-area conversion algorithms. Terminal harvest at week 5 provided comprehensive biomass data through destructive sampling of six randomly selected specimens per treatment. The harvested material underwent anatomical separation into aerial (shoots) and subterranean (roots) components, with aerial portions further subdivided into foliar and cauline fractions. Fresh mass determination occurred immediately following separation using an analytical balance (XPR205, Mettler Toledo, Columbus, OH, USA; precision ± 0.0001 g). Subsequent moisture extraction via temperature-controlled dehydration (70 °C for 72 h in a forced-air oven) preceded dry mass quantification. Dimensional measurements utilized digital calipers with 0.01 mm resolution, while mass determination employed calibrated analytical equipment with appropriate precision for the sample magnitude. All measurements adhered to standardized protocols to minimize operator variability and ensure data integrity across replications.

2.4. Quantification of Triterpene Glycosides

The analytical assessment of bioactive triterpene glycosides employed a modified chromatographic approach optimized for *C. asiatica* metabolite profiling [3]. Leaf sample collected at weekly intervals were immediately flash-frozen at -80 °C and subsequently lyophilized using a freeze dryer (ILShin Biobase, Dongducheon, Republic of Korea), followed by mechanical comminution to ensure sample homogeneity. The extraction protocol involved sonication-assisted solvent penetration, utilizing 50 mg of powdered leaf material suspended in 5 mL of aqueous methanol (HPLC-grade, 80% *v/v*) with controlled agitation (120 rpm, 60 min, 25 °C). The resulting homogenate underwent centrifugal separation (3500 rpm, 10 min) followed by microporous filtration (0.45 μ m PTFE membrane) to isolate the metabolite-containing supernatant. Chromatographic separation and quantification were conducted using high-performance liquid chromatography coupled with photodiode array detection (HPLC-PDA; Agilent 1260 Infinity II, Agilent Technologies, Santa Clara, CA, USA). The instrumental configuration incorporated a Nova-Pak C18 analytical column (4 μ m particle size, 3.9 $\times$ 150 mm dimensions; Waters Corporation, Milford, MA, USA) maintained at 30 °C. The mobile phase consisted of HPLC-grade water acidified with 0.1% formic acid (solvent A) and acetonitrile (solvent B) delivered according to an optimized gradient profile: 20–95% B (0–7 min), isocratic at 95% B (7–15 min), 95–20% B (15–21 min),

and re-equilibration at 20% B (21–25 min), with a constant flow rate of 1.3 mL/min. Detection was performed at 292 nm with concurrent spectral scanning (210–400 nm) for peak purity verification. Target analyte identification relied on retention time correlation with authenticated reference standards (madecassoside, asiaticoside, madecassic acid, and asiatic acid; $\geq 95\%$ purity, Sigma-Aldrich (Merck KGaA, St. Louis, MO, USA), while quantification employed external calibration curves (25–200 $\mu\text{g/mL}$) with linear regression analysis ($r^2 > 0.998$ for all compounds). The results were expressed as mg/g dry weight for each triterpene glycoside.

2.5. Statistical Analysis

The statistical framework incorporated multidimensional approaches tailored to the experimental design and research objectives. Temporal progression of growth parameters underwent repeated measures analysis of variance (RM-ANOVA) to differentiate time-dependent effects while accounting for within-subject correlation structures. The factorial treatment effects (light intensity $\times$ far-red supplementation) and their interactions were analyzed through two-way ANOVA with type III sum of squares computation. Post hoc discrimination of significant differences employed Tukey's honestly significant difference (HSD) procedure with family-wise error rate control at $\alpha = 0.05$. Relational patterns between growth metrics and phytochemical accumulation were explored through Pearson's correlation analysis with visualization via heat map representation. The mechanistic pathway connecting light treatment, morphological development, and bioactive compound synthesis was modeled using partial least squares structural equation modeling (PLS-SEM), providing quantification of both direct and mediated effects. Path coefficients were considered significant when their bootstrap-derived 95% confidence intervals excluded zero. Multivariate dimensionality reduction through principal component analysis (PCA) facilitated the holistic evaluation of treatment effects across the collective response variables. Statistical computations utilized the R software environment (R version 4.5.1 (The R Foundation for Statistical Computing, Vienna, Austria)) with specialized packages for multivariate analysis (vegan, lavaan, plspm), while graphical representation employed SigmaPlot version 16 (Systat Software Inc., San Jose, CA, USA). Statistical significance thresholds were established at $p < 0.05$ for all analytical procedures.

3. Results and Discussion

3.1. Morphological and Growth Responses

Various photosynthetic photon flux density (PPFD) levels and far-red light supplementation have distinct effects on the morphological development and growth of *C. asiatica*. Results from 5 weeks of cultivation demonstrated that far-red light supplementation (+FR) significantly altered the morphological development of *C. asiatica* (Figure 1).

Plants subjected to far-red (FR) light supplementation exhibited typical shade-avoidance responses, including enhanced vertical growth, petiole elongation, and leaf expansion. Notably, during weeks 2 to 3, FR-treated plants developed a more erect canopy architecture and exhibited a brighter green coloration. These morphological and visual changes are likely mediated by phytochrome B inactivation signaling pathways, as described by Smith and Whitelam [19], and may involve altered gene expression related to chloroplast development, as noted by Casal et al. [20]. In contrast, plants grown without FR supplementation displayed a rosette growth pattern with pronounced horizontal expansion, particularly under 100–150 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD. Active stolon development was frequently observed in these groups, a trait highlighted by Tewolde et al. [21] as beneficial for vegetative propagation in medicinal plant cultivation systems.

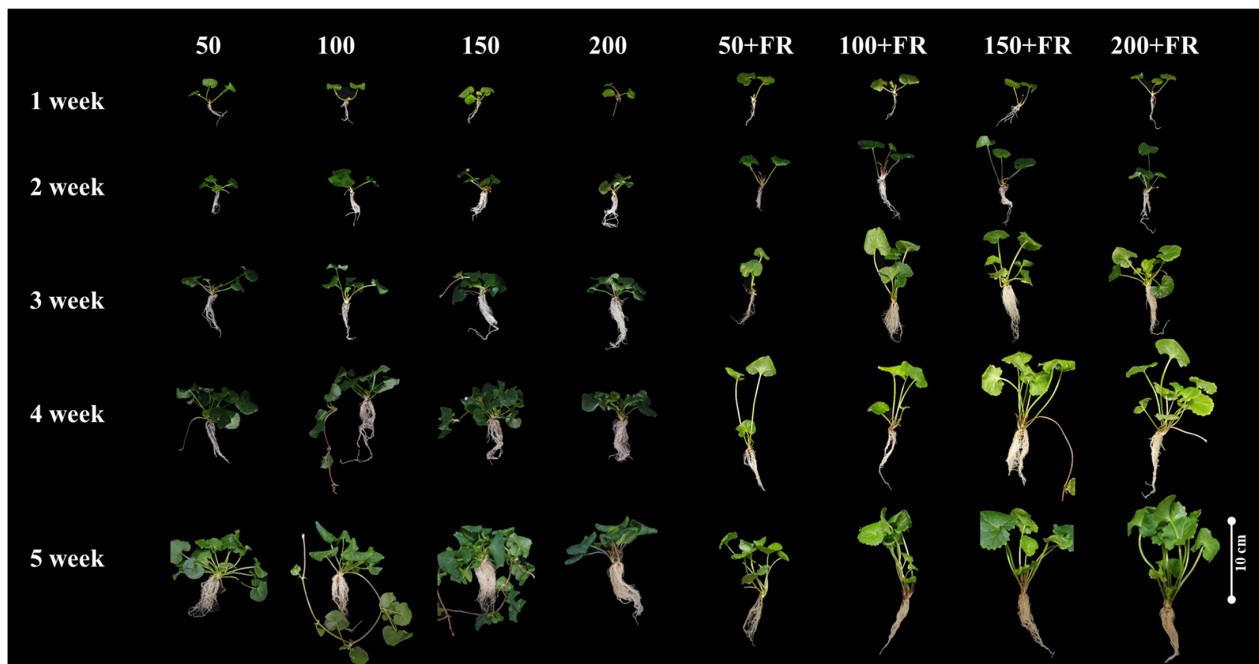


Figure 1. Morphological comparison of *Centella asiatica* growth over a 5-week period under eight light treatments: base light intensities (50, 100, 150, and 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) with and without far-red (FR) light supplementation. Plants grown under FR-supplemented conditions exhibited distinct morphological differences, particularly enhanced petiole elongation and increased leaf expansion compared to their non-FR counterparts.

From the first week of cultivation, plants receiving far-red light supplementation (+FR) began showing differences compared to the control groups without supplementation. By week 2, plants in the far-red light treatment groups (50FR, 100FR, 150FR, 200FR) exhibited distinct vertical growth and petiole elongation, with leaves displaying brighter and more vivid green coloration. In contrast, plants in treatments without far-red light supplementation (50, 100, 150, 200) maintained relatively dark green leaves and a compact form. These differences, as Hogewoning et al. [22] noted, demonstrate varying sensitivities to far-red light among plant species, with *C. asiatica*'s high sensitivity potentially related to its ecological adaptation as tropical understory vegetation. By weeks 3–4, the differences between treatments became more pronounced. Plants in the far-red light supplementation groups developed notably longer petioles and expanded leaf structures, particularly evident in the 100FR, 150FR, and 200FR treatment groups.

The vertical growth promotion and leaf area expansion due to far-red light supplementation may enhance spatial utilization efficiency and increase light capture area, potentially improving biomass productivity [10]. In contrast, treatments without far-red light supplementation formed dense rosette structures with more leaves and shorter petioles. Comparing final morphological characteristics at week 5, treatments without far-red light supplementation, especially the 100 and 150 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ groups, showed active stolon development and distinct horizontal expansion. Particularly in the 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ treatment, long and developed stolons were observed. In contrast, far-red light supplementation groups promoted vertical growth rather than stolon development, forming vertical structures with longer petioles and relatively fewer leaves (Figure 2).

Growth parameter analysis revealed that leaf number was significantly higher in treatments without far-red light supplementation, with the 150 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ treatment showing the maximum value of 21.33 ± 7.51 ($p < 0.05$). Conversely, far-red light treatment groups showed a marked decrease in leaf number, with the 50FR treatment recording the

minimum value of 6.00 ± 1.73 . This suggests that far-red light inhibits leaf formation in *C. asiatica*, a phenomenon previously reported in other rosette plant species [23].

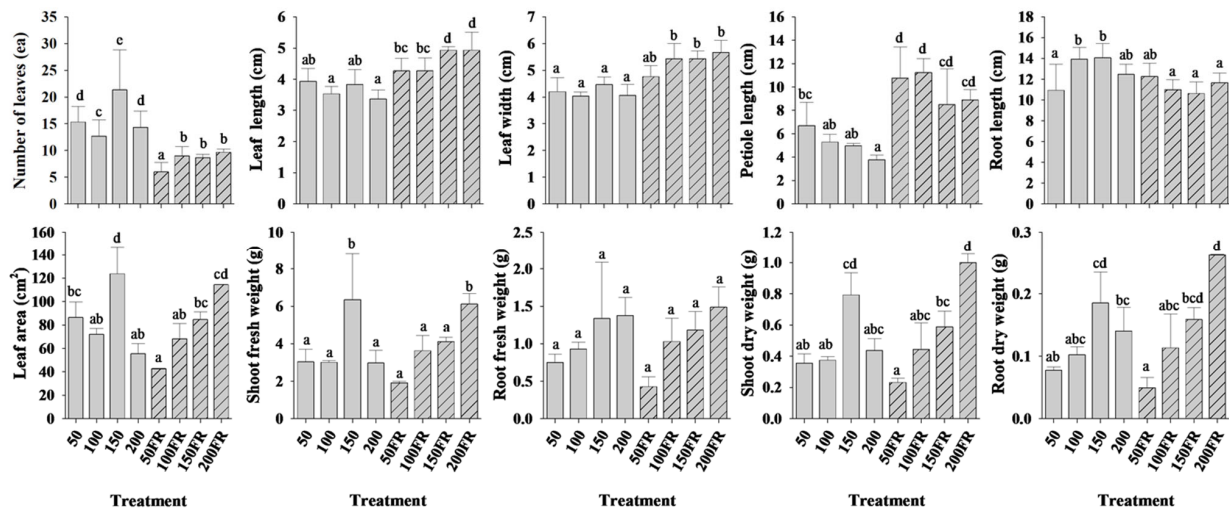


Figure 2. Effects of light intensity and far-red light supplementation on growth parameters in *Centella asiatica* after 5 weeks of treatment. Different letters above bars indicate significant differences among treatments according to Duncan's multiple range test at $p < 0.05$. Error bars represent the standard error of the mean ($n = 3$).

Leaf length, leaf width, and petiole length increased significantly with far-red light treatment. Notably, petiole length in far-red light treatment groups was approximately 1.6–2.8 times longer than control groups, representing a characteristic phenotype of far-red light-induced shade avoidance response. This morphological change can be understood as an adaptation strategy for understory plants in forest environments to detect shade from canopy plants and optimize light capture [24]. In contrast, root length tended to decrease with far-red light treatment, interpreted as part of an above-ground growth prioritization strategy.

A notable finding is that morphological changes in *C. asiatica* due to far-red light treatment interact with photosynthetic photon flux density to create complex effects. Leaf area was highest in the $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($123.72 \pm 23.60 \text{ cm}^2$) and 200FR ($114.47 \pm 0.29 \text{ cm}^2$) treatments, while lowest in the 50FR treatment ($42.67 \pm 0.38 \text{ cm}^2$). Similar to observations by Li and Kubota [25] in lettuce, far-red light supplementation reduced overall productivity at low PPFD levels ($50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) but increased biomass production at high PPFD levels ($200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). This suggests that morphological changes induced by far-red light can lead to productivity improvements when adequate photosynthetic input is available.

Fresh and dry weight measurements showed that above-ground fresh weight was highest in the $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($6.35 \pm 2.45 \text{ g}$) and 200FR ($6.12 \pm 0.55 \text{ g}$) treatments, while both above-ground and below-ground dry weights were highest in the 200FR treatment. This suggests that the combination of sufficient photosynthetic input and far-red light morphogenic effects created synergy to maximize biomass production [10]. Three-way ANOVA results showed highly significant main effects of far-red light (FR) and cultivation time (T) on most morphological parameters ($p < 0.001$) (Table 1). Particularly pronounced were the effects of far-red light on leaf number, leaf length, leaf width, and petiole length ($F = 86.08, 68.90, 62.34, 138.64$, respectively, $p < 0.001$), indicating that far-red light plays a crucial role in leaf morphology and structure. Additionally, significant two-way and three-way interactions were observed in many parameters, demonstrating that the effects of light intensity and far-red light are interdependent rather than independent. These statistical results confirm that *C. asiatica*'s growth and development respond very sensitively

to light environment conditions, particularly confirming the important role of far-red light in plant morphogenesis and resource allocation [26]. Far-red light supplementation altered resource allocation patterns in *C. asiatica*, promoting above-ground growth while relatively reducing below-ground growth. This represents a typical shade avoidance response mediated through phytochrome-mediated signaling pathways, interpreted as a strategic adaptation where plants prioritize allocating limited resources to above-ground growth [24]. Interestingly, the combination of high PPFD levels ($200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and far-red light supplementation (200FR) optimized the overall productivity of *C. asiatica*. The response to far-red light observed in *C. asiatica* highlights the need to note that plant species can show varied responses to far-red light. The high sensitivity to far-red light observed in this study may relate to *C. asiatica*'s ecological adaptation as tropical understory vegetation [27], reflecting survival strategies in its natural habitat. Additionally, far-red light supplementation resulted in a visually brighter green leaf appearance, suggesting potential alterations in chloroplast-related development. This visual observation may provide a basis for future research on light-responsive regulation of bioactive compound biosynthesis in *C. asiatica* [28].

These findings suggest that different light environment control strategies can be applied according to production objectives in the commercial cultivation of *C. asiatica*. For propagation-focused plant production, light environments with low far-red light ratios and moderate PPFD levels ($100\text{--}150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) may be suitable, promoting increased leaf number and stolon development advantageous for propagation [29]. Conversely, the combination of high PPFD ($200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and far-red light supplementation can be effective for maximizing biomass and functional component production. This combination maximizes above-ground biomass production, potentially increasing functional component yields.

3.2. Triterpene Glycoside Accumulation and the Influence of Light Conditions

The accumulation of triterpene glycosides was monitored over a 5-week period under varying far-red (FR) light supplementation treatments (50FR, 100FR, 150FR, and 200FR) while maintaining equivalent base light intensities (50, 100, 150, and $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Figure 3). Three-way ANOVA revealed highly significant effects of light intensity (L), time (T), and their interactions for all compounds ($p < 0.001$). Notably, FR treatment showed compound-specific effects, with significant direct effects on madecassoside and asiaticoside ($F = 38.76$, $p < 0.001$ and $F = 32.15$, $p < 0.001$, respectively), but non-significant direct effects on madecassic acid and asiatic acid ($F = 3.24$, NS and $F = 2.98$, NS, respectively) (Table 2).

These findings suggest that FR light may influence the biosynthesis of triterpene glycosides through specific regulatory pathways, while its effect on triterpene acids was not statistically significant under the conditions tested. At the beginning of the experiment (week 0), there were no significant differences in triterpene glycoside content among all treatment groups ($p > 0.05$). Initial concentrations were high for madecassic acid ($13.23 \pm 1.58 \text{ mg/g}$) and asiatic acid ($8.66 \pm 0.34 \text{ mg/g}$), while madecassoside ($3.31 \pm 0.09 \text{ mg/g}$) and asiaticoside ($2.52 \pm 0.10 \text{ mg/g}$) were detected at moderate levels. The total centelloside content was measured at $27.72 \pm 1.82 \text{ mg/g}$. After treatment initiation, madecassoside and asiaticoside exhibited similar temporal accumulation patterns across treatments, though the magnitude of changes varied with FR supplementation. Both glycosides showed a significant decrease at week 1 (declining to $0.06 \pm 0.00 \text{ mg/g}$ and $0.09 \pm 0.00 \text{ mg/g}$, respectively; $p < 0.001$ compared to baseline), followed by a gradual recovery in subsequent weeks. This initial decline may be interpreted as a temporary stress response occurring during the plant's adaptation process to changes in light environment [30].

Table 1. Analysis of variance (ANOVA) for the effects of light intensity (50, 100, 150, and 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), far-red light supplementation (FR), cultivation time (0–5 weeks), and their interactions on morphological and biomass parameters of *Centella asiatica*.

Parameters	Light Intensity (L)		Far-Red (FR)		Time (T)		L $\times$ FR		L $\times$ T		FR $\times$ T		L $\times$ FR $\times$ T	
	F-Value	Significance	F-Value	Significance	F-Value	Significance	F-Value	Significance	F-Value	Significance	F-Value	Significance	F-Value	Significance
Number of leaves	0.00	NS	86.08	***	120.59	***	0.00	NS	7.44	***	20.90	***	2.39	**
Leaf length	0.00	NS	68.90	***	86.43	***	0.00	NS	4.24	***	5.74	***	2.77	**
Leaf width	0.00	NS	62.34	***	65.05	***	0.00	NS	2.74	**	8.07	***	1.56	NS
Leaf area	0.00	NS	1.05	NS	309.23	***	0.00	NS	19.56	***	3.10	*	16.15	***
Petiole length	0.00	NS	138.64	***	77.18	***	0.00	NS	3.40	***	23.57	***	2.79	**
Root length	0.00	NS	11.66	***	199.58	***	0.00	NS	3.25	***	1.06	NS	2.14	*
Shoot fresh weight	0.00	NS	4.14	*	189.95	***	0.00	NS	16.46	***	1.01	NS	8.80	***
Root fresh weight	0.00	NS	1.28	NS	121.99	***	0.00	NS	18.02	***	0.82	NS	0.57	NS
Shoot dry weight	9.26	*	0.03	NS	14.92	*	0.00	NS	1.49	NS	0.01	NS	0.75	NS
Root dry weight	16.59	*	1.98	NS	33.62	**	0.00	NS	5.04	*	0.20	NS	0.67	NS

*, **, and *** indicate significance at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. NS: non-significant.

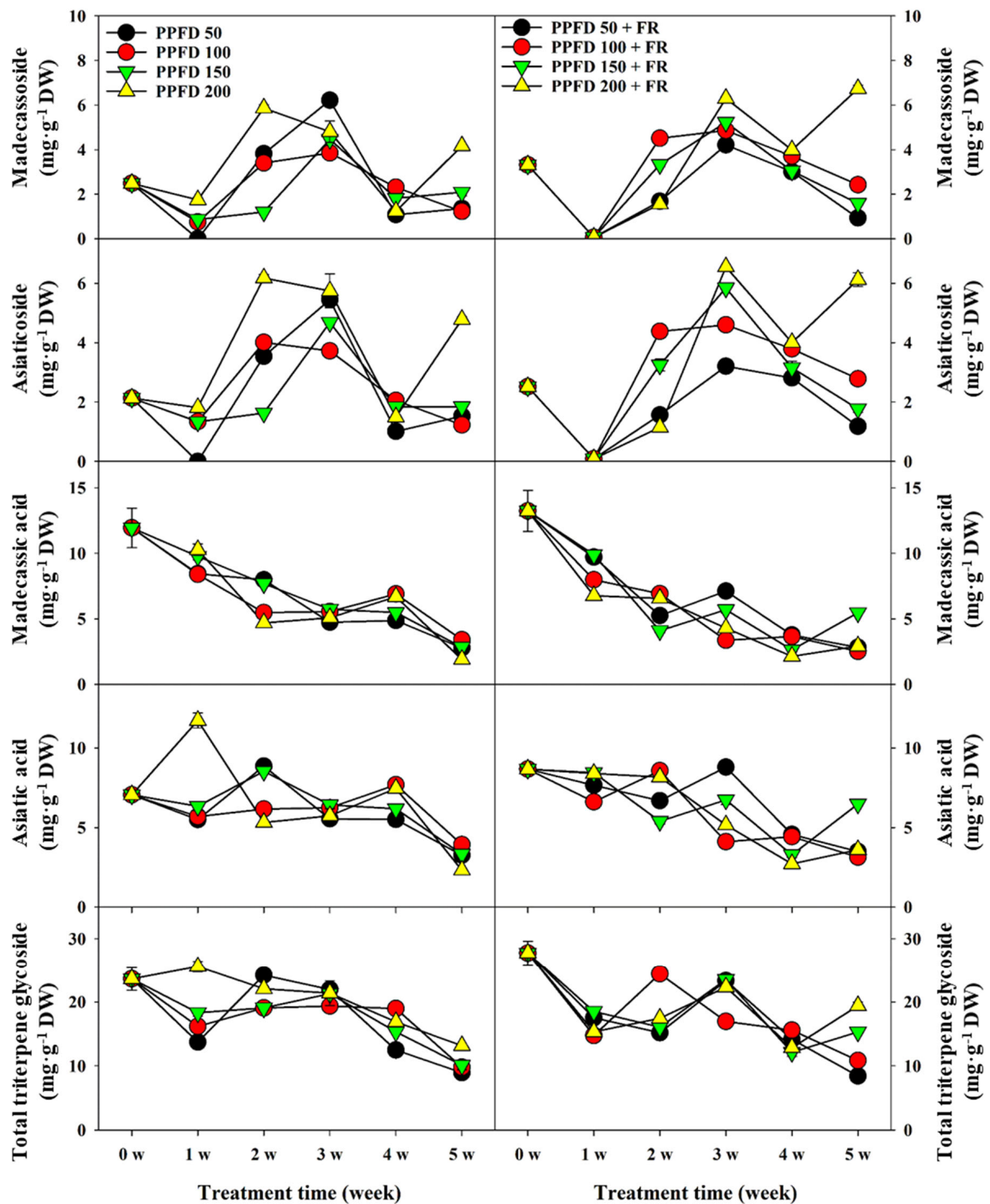


Figure 3. Temporal changes in triterpene glycoside content in *Centella asiatica* under different light intensities and far-red (FR) light supplementation during 5 weeks of cultivation. Values represent means $\pm$ SE (n = 3).

Table 2. Summary of three-way ANOVA for the effects of light intensity, far-red light supplementation, and time (0–5 weeks) on the accumulation of triterpene glycosides in *Centella asiatica*.

Parameters	Light Intensity (L)		Far-Red (FR)		Time (T)		L × FR		L × T		FR × T		L × FR × T	
	F-Value	Significance	F-Value	Significance	F-Value	Significance	F-Value	Significance	F-Value	Significance	F-Value	Significance	F-Value	Significance
Madecassoside	145.26	***	38.76	***	215.68	***	15.87	***	31.45	***	29.84	***	9.45	***
Asiaticoside	123.87	***	32.15	***	198.45	***	18.24	***	27.89	***	24.67	***	8.76	***
Madecassic acid	63.42	***	3.24	NS	167.29	***	7.63	***	19.76	***	5.84	**	4.32	**
Asiatic acid	78.95	***	2.98	NS	152.73	***	8.15	***	21.32	***	6.12	**	4.89	**
Total triterpene glycoside	89.34	***	11.43	**	178.96	***	12.78	***	25.65	***	14.29	***	6.53	**

*, **, and *** indicate significance at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. NS: non-significant.

Comparing treatments, the 200FR treatment resulted in the highest madecassoside content at week 5 (6.73 ± 0.17 mg/g), which was significantly higher than the control 200 base light intensity treatment (4.17 ± 0.03 mg/g) ($p < 0.001$). Similarly, asiaticoside reached its maximum content in the 200FR treatment at week 3 (6.55 ± 0.05 mg/g). In contrast to glycosides, triterpene acids (madecassic acid and asiatic acid) did not show significant direct responses to FR treatment, although treatment $\times$ time interactions were significant ($p < 0.01$). This suggests that FR light affects the temporal pattern of changes in triterpene acids rather than their biosynthesis directly. Notably, the 150 FR treatment displayed significantly higher levels of madecassic acid (5.46 ± 0.05 mg/g) and asiatic acid (6.48 ± 0.06 mg/g) at week 5 compared to other FR treatments ($p < 0.01$).

These differential accumulation patterns between glycosides and acids observed in both FR and non-FR treatments suggest that FR light may modulate the triterpene biosynthetic pathway by selectively enhancing glycoside accumulation, possibly via regulatory effects on glycosylation processes rather than overall pathway differentiation. Triterpene acids serve as precursors for glycosides [1], and our data suggest that FR light might enhance glycoside biosynthesis by promoting the glycosylation process through increased activity or expression of glycosyltransferases. This is supported by the pattern of sustained glycoside increase and gradual acid decrease observed in the 200FR treatment. Plants sense FR light through phytochrome B [19], and the resulting signaling may selectively upregulate genes related to glycosylation [31].

FR supplementation had differential effects on total centelloside content depending on light intensity. At low light intensity (50 FR), total centelloside content decreased continuously over time, reaching its lowest level at week 5 (8.42 ± 0.27 mg/g). At medium light intensity (100 FR), a transient increase was observed at week 2 (24.38 ± 0.95 mg/g) followed by a decline, while the 150 FR treatment reached peak accumulation at week 3 (23.50 ± 0.56 mg/g) and maintained substantial levels at week 5 (15.30 ± 0.14 mg/g). The 200 FR treatment exhibited relatively higher total centelloside content at both week 3 (22.30 ± 0.40 mg/g) and week 5 (19.38 ± 0.57 mg/g) compared to other treatments, although the differences with 100 FR and 150 FR were not substantial. A supplementary table (Table S1) is provided to present detailed mean and standard deviation values for each treatment and time point. The statistical significance of three-way interactions (L $\times$ FR $\times$ T) for all compounds ($p < 0.001$) indicates that the effect of FR light on triterpene glycoside accumulation depends on both light intensity and cultivation time. These results demonstrate that secondary metabolite biosynthesis in *C. asiatica* is regulated by complex environmental signal integration rather than the influence of a single factor. While the 200 FR treatment was most effective for madecassoside and asiaticoside accumulation, the 150 FR treatment showed superior results for maintaining madecassic acid and asiatic acid levels. These differential responses suggest that the phytochrome photoreceptor system may differentially affect various branches of the triterpene biosynthetic pathway [30].

The findings of this study have important practical implications for the commercial cultivation and optimization of triterpene glycoside production in *C. asiatica*. Since the 200 FR treatment was most effective for maintaining sustained total centelloside content, this can be directly applied to the development of cultivation protocols in plant factories or controlled environment agriculture. However, considering the differential effects on specific triterpene compounds, there is a need to customize light conditions according to the target compounds of interest. For example, the 200 FR treatment would be optimal if madecassoside and asiaticoside are the primary target compounds, while the 150 FR treatment might be more suitable if production of madecassic acid and asiatic acid is prioritized. While our data suggest that FR light may modulate glycoside biosynthesis through glycosylation-related mechanisms, the specific molecular regulators, such as glycosyltransferases, remain

to be identified. Future transcriptomic or enzyme activity studies are warranted to confirm these regulatory pathways and elucidate the gene networks involved.

The accumulation of triterpene glycosides was monitored over a 5-week period under varying far-red (FR) light supplementation treatments (50 FR, 100 FR, 150 FR, and 200 FR) while maintaining equivalent base light intensities (50, 100, 150, and 200). Three-way ANOVA revealed highly significant effects of light intensity (L), time (T), and their interactions for all compounds ($p < 0.001$). Notably, FR treatment showed compound-specific effects, with significant direct effects on madecassoside and asiaticoside ($F = 38.76$, $p < 0.001$ and $F = 32.15$, $p < 0.001$, respectively), but non-significant direct effects on madecassic acid and asiatic acid ($F = 3.24$, NS and $F = 2.98$, NS, respectively) (Table 2).

These findings suggest that FR light may influence the biosynthesis of triterpene glycosides through specific regulatory pathways, while its effect on triterpene acids was not statistically significant under the conditions tested. At the beginning of the experiment (week 0), there were no significant differences in triterpene glycoside content among all treatment groups ($p > 0.05$). Initial concentrations were high for madecassic acid (13.23 ± 1.58 mg/g) and asiatic acid (8.66 ± 0.34 mg/g), while madecassoside (3.31 ± 0.09 mg/g) and asiaticoside (2.52 ± 0.10 mg/g) were detected at moderate levels. The total centelloside content was measured at 27.72 ± 1.82 mg/g. After treatment initiation, madecassoside and asiaticoside exhibited similar temporal accumulation patterns across treatments, though the magnitude of changes varied with FR supplementation. Both glycosides showed a significant decrease at week 1 (declining to 0.06 ± 0.00 mg/g and 0.09 ± 0.00 mg/g, respectively; $p < 0.001$ compared to baseline), followed by a gradual recovery in subsequent weeks. This initial decline may be interpreted as a temporary stress response occurring during the plant's adaptation process to changes in the light environment [31].

Comparing treatments, the 200 FR treatment resulted in the highest madecassoside content at week 5 (6.73 ± 0.17 mg/g), which was significantly higher than the control 200 base light intensity treatment (4.17 ± 0.03 mg/g) ($p < 0.001$). Similarly, asiaticoside reached its maximum content in the 200 FR treatment at week 3 (6.55 ± 0.05 mg/g). In contrast to glycosides, triterpene acids (madecassic acid and asiatic acid) did not show significant direct responses to FR treatment, although treatment $\times$ time interactions were significant ($p < 0.01$). This suggests that FR light affects the temporal pattern of changes in triterpene acids rather than their biosynthesis directly. Notably, the 150 FR treatment displayed significantly higher levels of madecassic acid (5.46 ± 0.05 mg/g) and asiatic acid (6.48 ± 0.06 mg/g) at week 5 compared to other FR treatments ($p < 0.01$).

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3.3. Correlation and PCA Analysis

Principal Component Analysis (PCA) was performed to explore the complex relationships between triterpene glycoside accumulation and growth parameters over the 5-week cultivation period (Figure 4). Two separate analyses were conducted based on treatment conditions: base light intensity treatments (50, 100, 150, and 200 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and far-red supplementation treatments (50 FR, 100 FR, 150 FR, and 200 FR $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).

Compared to base light treatments (Figure 4A), far-red supplementation (Figure 4B) altered the relationship patterns between morphological traits and triterpene glycoside accumulation, as visualized by distinct shifts in principal component loading vectors. Although no formal statistical test was performed on PCA group separation, the increased proportion of explained variance (Dim1: 65.9%) indicates stronger covariance among variables under FR conditions. Weeks 1–2 samples are positioned in the negative direction of Dim1, while weeks 4–5 samples are distributed toward the positive direction, indicating a clear time-dependent progression in plant development and metabolite accumulation. Triterpene compounds demonstrated distinct clustering patterns under base light intensity conditions. Glycosidic triterpenes (madecassoside and asiaticoside) and total centelloside clustered together in the positive direction of Dim2, while aglycone triterpenes (madecassic acid and asiatic acid) were positioned in the negative direction of Dim1, showing clear separation from their glycosidic counterparts. Growth parameters, including leaf area, number of leaves, shoot fresh weight, and leaf width, were positioned along the positive direction of Dim1, indicating their association with plant development in later growth stages.

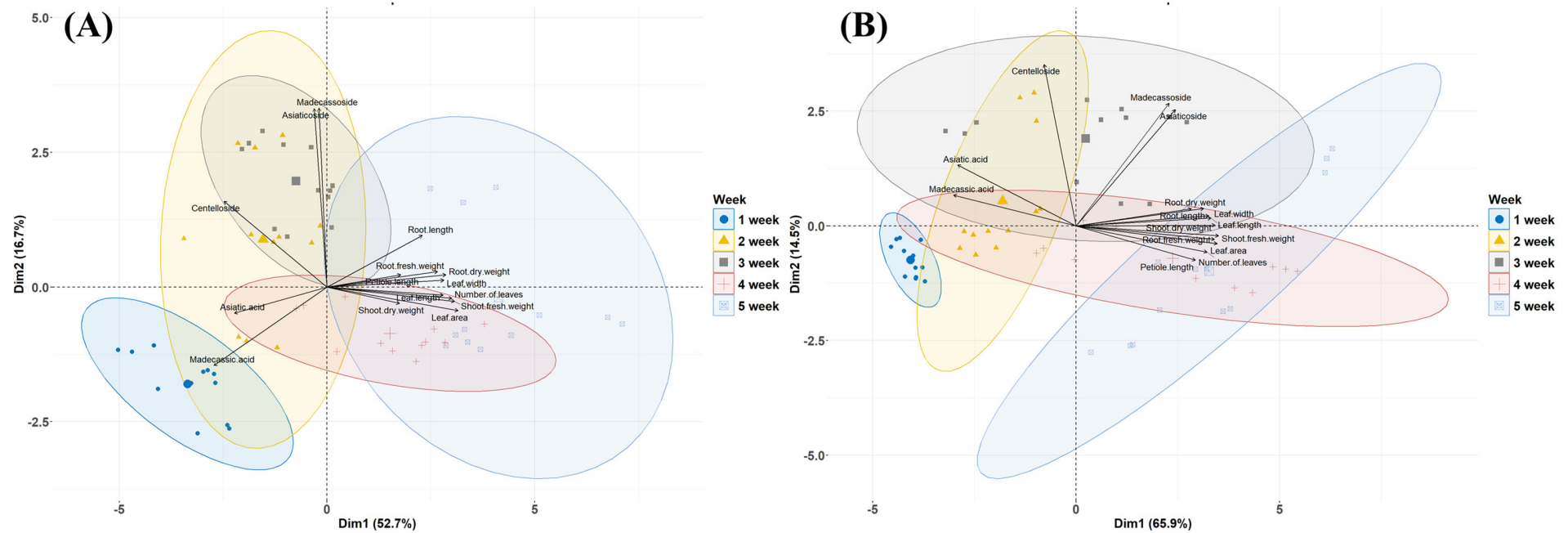


Figure 4. Principal component analysis (PCA) biplots illustrating the temporal dynamics of triterpene glycoside accumulation and morphological parameters in *Centella asiatica* under different light treatments over a 5-week cultivation period: (A) base light intensity treatments (50, 100, 150, and 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and (B) far-red supplementation treatments with 1:0 R ratio (50 FR, 100 FR, 150 FR, and 200 FR $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Data points represent individual samples ($n = 3$ for each treatment) with confidence ellipses grouped by week.

Under far-red supplementation treatments (Figure 4B), the relationship patterns changed significantly, with the first two principal components explaining a higher proportion of variance. Dim1 alone accounted for 65.9% of the total variance, demonstrating that far-red light induced more coordinated changes in both growth and secondary metabolite accumulation. The temporal clustering of samples remained evident, with week 1 samples clearly separated from later weeks, particularly week 5 samples, which showed the greatest distance along Dim1. In the far-red treatment group, centelloside and related glycosidic triterpenes (madecassoside and asiaticoside) were positioned in the positive direction of Dim2, while root dry weight, shoot dry weight, and leaf metrics (leaf length, leaf width, leaf area) clustered together along the positive direction of Dim1. This suggests that far-red light strengthens the association between plant biomass accumulation and specific morphological traits during later growth stages [8]. A notable difference between the two treatment types was the altered positioning of growth parameters relative to triterpene compounds. Under far-red supplementation, the number of leaves and petiole length showed stronger association with plant development metrics compared to base light treatments, suggesting that far-red light modifies resource allocation patterns between vegetative growth and secondary metabolite production. The temporal progression visualized through weekly clustering in both PCA biplots highlights the dynamic nature of growth and triterpene accumulation in *C. asiatica*. Early growth stages (weeks 1–2) were characterized by higher relative levels of aglycone triterpenes (madecassic acid and asiatic acid), while later stages (weeks 4–5) showed increased association with glycosidic triterpenes (madecassoside and asiaticoside) and enhanced growth parameters. These multidimensional analysis results emphasize the importance of both light intensity and spectral quality for optimizing triterpene glycoside production in *C. asiatica*. The temporal dynamics revealed through PCA provide valuable insights for determining optimal harvest timing and cultivation conditions for the commercial production of specific bioactive compounds [4].

Pearson correlation analysis revealed intricate relationships between growth parameters and triterpene compounds (Figure 5). The correlation matrix elucidated distinct patterns of association between biomass allocation metrics and secondary metabolite accumulation. Morphological growth parameters exhibited strong intercorrelations, with leaf length and leaf width demonstrating a particularly robust positive correlation ($r = 0.97$, $p < 0.001$). The observed strong positive correlation between leaf area and shoot fresh weight ($r = 0.99$, $p < 0.001$) substantiates the critical role of photosynthetic surface area in determining aboveground biomass formation [3].

Triterpene compounds demonstrated compound-specific correlation patterns. The glycosidic triterpenes (madecassoside and asiaticoside) were strongly correlated with each other ($r = 0.97$, $p < 0.001$), as were their respective aglycones, madecassic acid, and asiatic acid ($r = 0.77$, $p < 0.001$). These findings suggest coordinated regulation of biosynthetic pathways within structurally similar triterpene compounds. The relationship between growth parameters and triterpene accumulation provided significant physiological insights into resource allocation trade-offs. Madecassic acid exhibited significant negative correlations with multiple growth parameters, most notably with root length ($r = -0.87$, $p < 0.001$). Similarly, asiatic acid displayed moderate to strong negative correlations with key growth indices ($r = -0.55$ to -0.65 , $p < 0.001$). These results align with the growth–defense balance hypothesis, demonstrating the trade-off between primary metabolism for biomass accumulation and secondary metabolism for defense-related compounds. Notably, madecassoside and asiaticoside, unlike other triterpene compounds, showed weak positive correlations with certain growth parameters (particularly leaf width, $r = 0.33$ and 0.40 , $p < 0.05$). This differential correlation pattern suggests that specific secondary metabolite biosynthetic pathways may be selectively activated depending on plant developmental stages or en-

vironmental conditions, warranting further investigation through metabolomic profiling studies. Centelloside exhibited moderate negative correlations with overall growth parameters ($r = -0.42$ to -0.58 , $p < 0.01$). This reflects the physiological mechanism by which plants redistribute carbon resources between growth and defense mechanisms in response to environmental stressors or cultivation conditions, interpretable within the context of optimal defense theory. These findings provide crucial baseline data for developing cultivation strategies that optimize the balance between biomass production and bioactive compound content in medicinal plants.

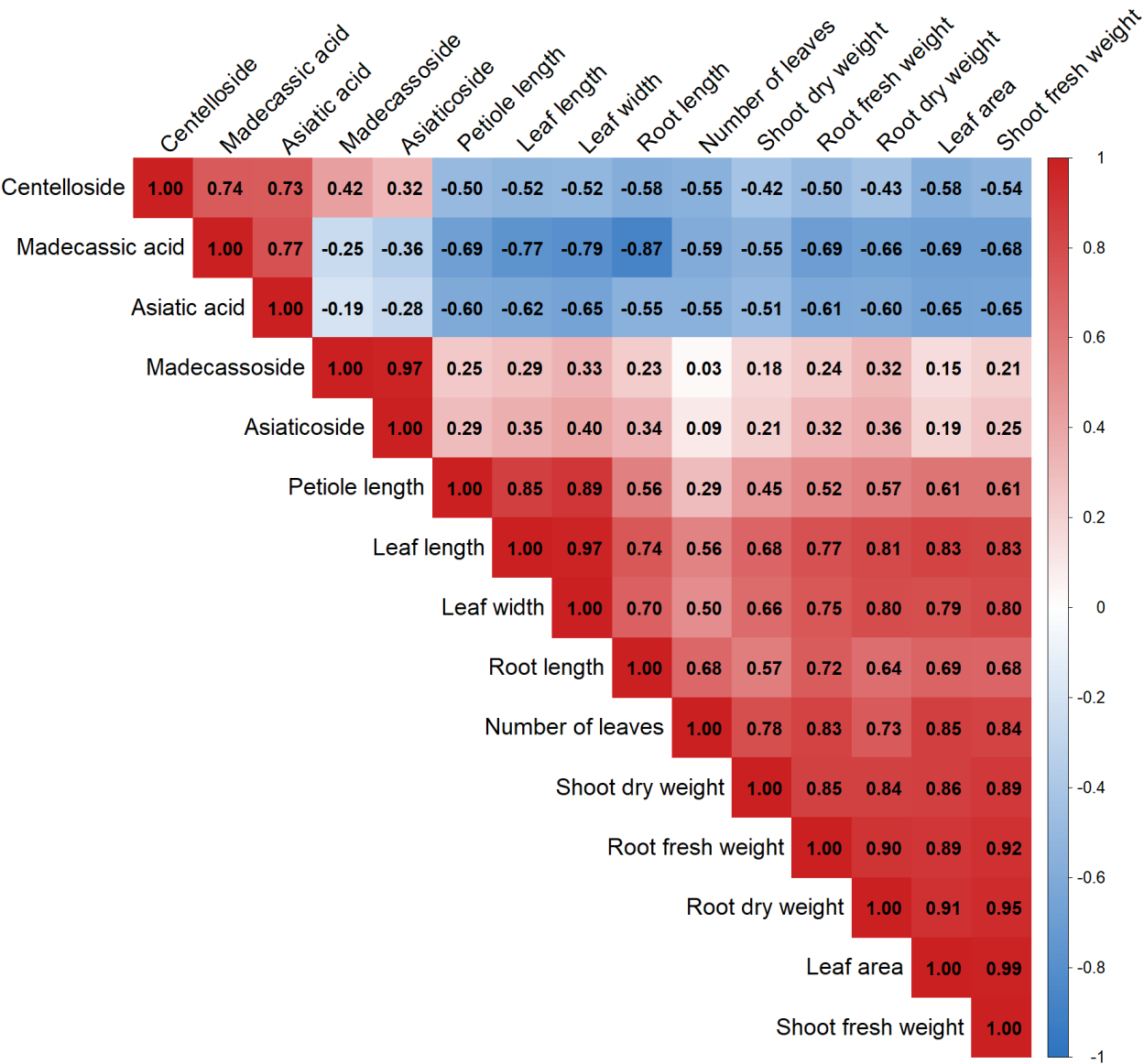


Figure 5. Correlation heatmap showing the relationships between growth parameters and triterpene glycoside accumulation in *Centella asiatica* cultivated under different light intensity and far-red supplementation treatments over 5 weeks (n = 3 per treatment). Red indicates positive correlation and blue indicates negative correlation, with color intensity proportional to correlation coefficient.

4. Conclusions

We identified compound-specific responses to far-red (FR) light supplementation in *C. asiatica*, with glycosides (madecassoside and asiaticoside) showing significant direct effects to FR light ($p < 0.001$), while acids (madecassic acid and asiatic acid) responded only through interactions with other factors. Three-way ANOVA confirmed significant

interactions between light intensity, FR supplementation, and time for all studied triterpene compounds, revealing complex regulatory mechanisms within the triterpene biosynthetic pathway. The highest light intensity with FR supplementation (200 FR) resulted in the least reduction in total centelloside content over the cultivation period, maintaining significantly higher levels at week 5 (19.38 ± 0.57 mg/g; $p < 0.001$) compared to all other treatments. In contrast, the 150 FR treatment better preserved triterpene acid levels (madecassic acid: 5.46 ± 0.05 mg/g; asiatic acid: 6.48 ± 0.06 mg/g at week 5). Principal component analysis demonstrated that FR supplementation coordinates growth and secondary metabolite accumulation more effectively than base light treatments alone, suggesting modified resource allocation between vegetative growth and phytochemical production. The temporal dynamics of triterpene accumulation revealed distinct patterns, with an initial decrease at week 1 followed by recovery and compound-specific accumulation trends. This indicates adaptation processes in response to changing light environments and suggests strategic timing for harvest to optimize specific bioactive compound yields. Based on our results, we conclude that FR light supplementation can be effectively utilized to enhance triterpene glycoside production in *C. asiatica*, with light intensity and spectral composition being critical factors for optimizing specific compound profiles. For commercial cultivation targeting glycosidic triterpenes, high-intensity light ($200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) with FR supplementation provides optimal conditions, while moderate intensity ($150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) with FR is more suitable for triterpene acid production. However, considering that total glycoside content was highest at the beginning of the experiment, early harvesting before a substantial decline may represent a more efficient strategy for maximizing glycoside yield per unit biomass and cultivation time.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/horticulturae11070728/s1>, Table S1: Morphological and Biomass Responses of *Centella asiatica* to Varying Photosynthetic Photon Flux Density (PPFD) and Far-Red Light Supplementation after 5 Weeks of Cultivation; Table S2: Changes in Triterpenoid Compound Contents of *Centella asiatica* under Varying Photosynthetic Photon Flux Density (PPFD) and Far-Red Light Supplementation during 5 Weeks of Cultivation.

Author Contributions: Conceptualization, J.W.S. and J.G.L.; methodology, J.W.S. and J.G.L.; software, Y.K.S. and J.G.L.; validation, J.W.S. and J.G.L.; formal analysis, Y.K.S. and J.G.L.; investigation, J.W.S. and J.G.L.; resources, Y.K.S. and J.G.L.; data curation, J.W.S. and J.G.L.; writing—original draft preparation, J.W.S., Y.K.S. and J.G.L.; writing—review and editing, all authors; visualization, J.W.S. and J.G.L. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: All the data generated during the study are presented within the article. The raw data are available from the corresponding author upon reasonable request.

Conflicts of Interest: The authors declare no conflicts of interest.

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