Environmental and Experimental Botany 229 (2025) 106059

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Research paper

Decreasing R:FR ratio in a grow light spectrum increases inflorescence yield but decreases plant specialized metabolite concentrations in *Cannabis sativa*

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ARTICLE INFO

Dataset link: Cannabis sativa, R:FR ratio, cannabinoids and yield

Keywords:
Cannabis sativa
R:FR ratio
far-red
cannabinoid
CBDA
terpene
spectrum

ABSTRACT

Cultivation of *Cannabis sativa* for recreational and pharmaceutical purposes has been increasing significantly in recent years due to legalization in many countries. Cultivation takes place regularly indoors under varying artificial lighting sources. There is a lack of scientific knowledge on the effect of light spectrum on the *C. sativa* morphology, yield, and quality, especially the cannabinoid and terpene concentrations in the female inflorescences in indoor environments. Furthermore, only a handful of the spectra studies conducted so far study or discuss the effect of far-red radiation, while the effect of other wavelengths, such as UV or blue, has gained more attention. This study had two aims: (1) to examine plant morphology and inflorescence yield under varying red to far-red ratio (R:FR) treatments with equal photon flux densities (380–780 nm), and (2) to examine the possible relationship of the cannabinoid and terpene concentrations with the spectrum's R:FR ratio, Plant material was collected as cuttings from *C. sativa* 'Finola' mother plants and grown under 18 h photoperiod before transferring them under the light treatments for 49 days (550 μmol m^{-2} s^{-1}, 12 h/12 h dark/light). Light treatments were created with two types of LED fixtures, white spectrum (380–780 nm) and far-red (730 nm), which were used to create four R:FR ratio treatments; R:FR 3, 5, 9, and 12. Plant morphology was affected by the R:FR ratio; under the lowest R:FR (3) treatment plants were tallest, and the apical inflorescence dry weight decreased linearly with increasing R:FR ratio. The concentrations of many terpenes and cannabinoids including cannabidiolic acid (CBDA), tetrahydrocannabinolic acid (THCA), and cannabigerolic acid (CBGA), increased with increasing R:FR ratio. In conclusion, spectra with different R:FR ratios can be used as a tool at different growth phases to modify the plant morphology, inflorescence yield, and cannabinoid and terpene concentrations.

1. Introduction

The female inflorescence is the most valuable plant part in *C. sativa*, with over 500 plant specialized metabolites (PSM) identified. These include terpenes, flavonoids, and cannabinoids, which are stored in the trichomes (Livingston et al., 2020; Desaulniers Brousseau et al., 2021). For centuries, *C. sativa* has been utilized in traditional medicine. Today, it's potential and proven pharmaceutical properties in the modern medicine have also been recognized and studied for a wide variety of medical conditions (Russo, 2011; Boyaji et al., 2020; Bautista et al., 2021). While it has been acknowledged that chemical non-uniformity within the plant exists depending on the position where plant material is being collected from, the uniformity of raw material is an important standard in the pharmaceutical industry (Danziger and Bernstein, 2021b; Bernstein et al., 2019; Reichel et al., 2022). Therefore, it is essential to understand the effects of the cultivation environment and growing conditions on the inflorescence yield and chemical composition to meet the requirements of high inflorescence biomass together with as uniform and predictable raw material quality as possible.

Cannabinoid and terpene concentrations are primarily predetermined by the plant genotype, but environmental conditions and cultivation techniques also play a role. For example, photoperiod (Ahrens et al., 2023), temperature (Chandra et al., 2008), light intensity (Chandra et al., 2008), light spectrum (Magagnini et al., 2018; Reichel

Abbreviations: CBD, cannabidiol; CBDA, cannabidiolic acid; CBGA, cannabigerolic acid; LFI, leaf flavonoid index; PAR, photosynthetically active radiation; PFD, photon flux density; PPFD, photosynthetic photon flux density; PSM, plant specialized metabolites; THCA, tetrahydrocannabinolic acid; R:FR, red to far-red.

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https://doi.org/10.1016/j.envexpbot.2024.106059
Received 7 August 2024; Received in revised form 15 November 2024; Accepted 3 December 2024
Available online 6 December 2024

et al., 2021, 2022; Rodriguez-Morrison et al., 2021), fertilization (Saloner and Bernstein, 2021, 2022), irrigation or drought treatments (Park et al., 2022; Morgan et al., 2024), and different pruning methods (Dilena et al., 2023) have been shown to affect the inflorescence yield and the chemical composition of female inflorescences. Among the above-mentioned environmental factors, light is considered to be one of the most important elements in indoor cultivation facilities.

One of the first studies comparing the morphology and floral cannabinoid concentrations of *C. sativa* under different types of artificial light sources, two LED spectra and an HPS light source, was published in 2018 by Magagnini et al. After that, many other studies have confirmed that *C. sativa* morphology, inflorescence yield, and chemical properties can be influenced with light spectrum (Magagnini et al., 2018; Reichel et al., 2021, 2022; Danziger and Bernstein, 2021a; Jenkins, 2021; Kotiranta et al., 2024). However, so far none of the studies have concentrated on far-red or R:FR specifically.

Light signals are perceived by different photoreceptors, such as the red and far-red absorbing phytochromes, and the blue and UV-A absorbing cryptochromes and phototropins (Franklin, 2008). Phytochromes exist in two formats: the red-light-absorbing, inactive, Pr form, and the active, far-red-light-absorbing, Pfr form. The ratio between red and far-red photons in the ambient light spectrum affects the equilibrium between the two phytochrome forms, which determines multiple different responses in plants, such as the shade avoidance syndrome (SAS) under low R:FR conditions (Brown et al., 1995; Smith and Whitelam, 1997; Li and Kubota, 2009; Ballaré and Pierik, 2017). SAS symptoms include elongated stem and leaves, reduced leaf chlorophyll concentrations, increased apical dominance, and reduced harvestable yield in many species (Franklin, 2008), symptoms which have been recently described for *C. sativa* as well (Kotiranta et al., 2024). SAS symptoms develop in low R:FR conditions when the inactive Pr stabilizes the phytochrome interacting factors (PIFs), which promote the expression of genes involved in auxin biosynthesis (Iglesias et al., 2018). The signal of low R:FR ratio results in an increase in auxin levels in leaves and its transport to stem and epidermal tissues, thereby promoting growth.

While SAS symptoms under very low R:FR ratio can be associated with excessive stem elongation and decreased yields (Kotiranta et al., 2024), a more moderate substitution of PAR with far-red could offer tools to impact plant growth positively. For example, far-red has been shown to increase the individual plant cell size and enhance cell division rate, resulting in an increase in the leaf area in cucumber seedlings (*Cucumis sativus*) (Li et al., 2024). Far-red induced leaf-area expansion has been previously reported also with lettuce (*Lactuca sativa*) (Zhen and Bugbee, 2020a), geranium (*Pelargonium* x *hortorum*), and snapdragon (*Antirrhinum majus*) (Park and Runkle, 2017). Increased leaf area, induced by far-red radiation, provides more leaf surface area for photon capture which could potentially lead to a higher light use efficiency (LUE) and eventually higher yield, something which has already been demonstrated with lettuce (Jin et al., 2021; Carotti et al., 2024) but not yet with *C. sativa*.

In addition to the improved morphology for enhanced photon capture, the spectrum could also impact yield formation via photosynthesis rate or dry mass partitioning to reproductive parts. Although photosynthesis rate under sole far-red radiation has been shown to be low (Emerson and Lewis, 1943), the rate increases when far-red is given additionally to photosynthetically active radiation (PAR), as demonstrated with lettuce (Zhen and van Iersel, 2017). Additionally, far-red has been shown to increase dry mass partitioning to the reproductive plant parts, such as fruits in tomato (*Solanum lycopersicum*) (Ji et al., 2020; Kalaitzoglu et al., 2019; Vincenzi et al., 2024). The potential yield increase through moderate substitution of PAR with far-red via increased photosynthesis rate or dry mass partitioning to reproductive plant parts (female inflorescences) has not yet been reported in literature for *C. sativa*.

Besides the morphological changes induced by light spectrum, the floral PSM concentrations in *C. sativa* have been shown to change according to light quality, although results have been contradictious and genotype dependent. For example, short wavelength radiation, i.e. blue and ultra-violet (UV) radiation, increased the concentrations of all measured cannabinoids in the study by Magagnini et al. (2018), THCV and myrcene concentrations in Kotiranta et al. (2024), and THC concentration in two out of the three tested genotypes in Jenkins (2021), while in Rodriguez-Morrison et al. (2021), UV radiation caused a reduction or had no impact on the cannabinoid concentrations, depending on the tested genotype. Until now, the effect of far-red radiation *an sich,* or R:FR ratio, on inflorescence yield and quality has received less attention than short wavelength radiation. Most of the studies discussing the effect of far-red on PSM concentrations so far (Magagnini et al., 2018; Danziger and Bernstein, 2021a; Reichel et al., 2021, 2022) could only hypothesize on the relationship between measured plant responses and the amount of far-red radiation, or R:FR ratio, as the spectra used in these experiments differed also in other wavelength areas besides far-red.

Spectrum mediated changes in the plant metabolism are induced via activation or inactivation of photoreceptors leading to induction of light signaling intermediates. These intermediates include transcription factors which promote the expression of genes encoding key enzymes involved in metabolic pathways promoting biosynthesis of different PSM such as terpenes, phenolics, and flavonoids (Lingwan et al., 2023). For example, the spectrum's R:FR ratio determines the phytochrome equilibrium, which in turn impacts the function of PIFs involved in the methylerythritol phosphate (MEP) pathway linked to both cannabinoid and monoterpene biosynthesis pathways (Chenge-Espinosa et al., 2018; Desaulniers Brousseau et al., 2021). In low R:FR, phytochromes shift to their inactive Pr form, promoting the accumulation of PIFs, which act as suppressors of many genes in the MEP pathway, reducing the biosynthesis of cannabinoids and terpenes (Chenge-Espinosa et al., 2018). Previously, far-red radiation has been shown to down-regulate PSM pathways for example in *Arabidopsis thaliana* (Cargnel et al., 2014) and in lettuce (Li and Kubota, 2009), shown as decreased concentrations of indole glucosinolates and camalexin in *A. thaliana*, and anthocyanins in lettuce. The impact of far-red on cannabinoids, flavonoids, or terpenes in *C. sativa* studied with spectra differing only in their far-red content has previously been published only in Kotiranta et al. (2024). The study demonstrated that a spectrum's low R:FR ratio (R:FR 1), resulted in decreased concentrations of cannabinoids CBD, THCVA, and CBGA while no difference was detected in THCA, CBDVA, or CBDA. In the same study, the concentrations of all tested monoterpenes and a sesquiterpene, β-farnesene, decreased under the low R:FR treatment. The experiment had only two treatments, R:FR 1 and R:FR 11, leaving open the question whether the far-red induced reduction in PSM is notable only under very low R:FR conditions and whether the response of the PSM concentrations to the spectrum's R:FR is linear.

This study aimed to address two main objectives related to the effects of the R:FR ratio on *C. sativa*. The first objective was to investigate how spectra treatments with varying R:FR ratios and equal photon flux densities (PFD) (380–780 nm), affect inflorescence yield, plant morphology, operational photosynthesis rate, and LUE. The second objective was to test the hypothesis whether the inflorescence cannabinoid, terpene, and flavonoid concentrations respond to the spectrum's R:FR ratio.

2. Materials and methods

The effect of light spectrum, specifically the R:FR ratio, on morphology, inflorescence yield, and PSM accumulation on *C. sativa* was studied in a research greenhouse at the University of Helsinki, Finland, between 14.6.–4.9.2022.

2.1. Plant material and growing conditions

Plant material for the experiment was obtained as apical stem cuttings taken from approximately four-month-old genetically identical *C. sativa* 'Finola' mother plants. Total of 200 cuttings, each ~15 cm in height with three to four leaves, were taken between 14.6.–16.6.2022 and rooted in Sublime cubes (BVB substrates, De Lier, The Netherlands) in plastic rooting containers with transparent cover (container measurements L 40 cm x W 20 cm x H 20 cm). Light intensity during the rooting period was measured with a spectrometer (UPRTek MK350S, Zhunan township, Taiwan) at the container surface level between 380 and 780 nm and set to 150 μmol $m^{-2}s^{-1}$ (RF600–6, Solray385, Valoya Oy, Helsinki, Finland), spectrum during the rooting period was the same as treatment R:FR 12 spectrum (Fig. 1). Greenhouse climate was controlled by an automated climate control system (Priva, De Lier, The Netherlands); photoperiod was set to 18 h per day, ambient temperature to 24/22 °C day/night, relative humidity (RH) to 60 %/50 % day/night, and ambient CO_2 during the experiment was ~400 ppm. Cuttings were irrigated with tap water on the day they were cut and every third days after that and misted daily.

Nineteen days after taking the cuttings (DAC), 126 homogeneous rooted cuttings were potted into ø 12-cm pots filled with fertilized peat (pH 6, EC 2.1 dS m^{-1}) (AirBoost 640 R8421, Kekkilä-BVB, Vantaa, Finland), irrigated with tap water and placed on greenhouse benches (1.2 × 4.6 m). The rooted cuttings were grown in a greenhouse compartment under similar conditions as during the rooting period except that light intensity was raised to 350 μmol $m^{-2}s^{-1}$ at canopy level.

After 11 days (30 DAC), 108 homogeneous plants were repotted into 2-liter pots, irrigated with tap water, light intensity raised to 400 μmol $m^{-2}s^{-1}$, and transferred under the light treatments (start of the experiment = SOE) for 49 days.

2.2. Experimental design and light treatments

Plants were cultivated on three benches, each 1.2 × 4.6 m in size. The experiment was conducted as randomized complete block design with three replicate blocks (benches) containing each of the four light treatments once per block (Fig. S1A). Benches were divided into 1.2 × 1.2 m smaller plots, which were separated with white plastic sheets to prevent light contamination between the treatments. Each replicate plot contained 9 plants, thus 27 plants in total per light treatment and 7.5 plants m^{-2}. Pots were circulated within the plot weekly during the experiment to equalize growing conditions (Fig. S1B).

The experiment included four light treatments where the target R:FR ratio of the light spectrum was 3, 5, 9, or 12 (Table 1). In treatment R:FR 12, a white LED spectrum was used (RF600–6, Solray385, Valoya Oy, Helsinki, Finland) (Fig. 1). In treatments R:FR 3, 5, and 9 the same white LED spectrum was used together with FR LED fixtures with a peak wavelength at 730 nm (C65, Valoya Oy, Helsinki, Finland) to create the different R:FR ratio treatments (Fig. 1). Light intensity and R:FR ratio were measured weekly at canopy height and adjusted individually per plot. The R:FR ratio was calculated according to Sellaro et al. (2010), and in addition the FR fraction was calculated for each treatment, as suggested by Kusuma and Bugbee (2021) (Table 1). Spectral photon irradiance was measured with an array spectroradiometer (Maya2000 Pro Ocean Optics, Dunedin, Fl, USA; D7-H-SMA cosine diffuser, Bentham Instruments Ltd, Reading, UK). Measurements were taken from each replicate plot at canopy height, recorded within the wavelength range from 280 to 900 nm, and processed in R (R Core Team, 2017), using the photobiology packages developed for spectral analysis (Aphalo, 2015). The means of the spectral distribution of the three treatment replicates are presented in Table 1 and spectral graphs of the treatments in Fig. 1.

2.3. Growing conditions during the experiment

Photoperiod was set to 12 h for flowering induction and climate conditions were the same as during the propagation phase. Irrigation and nutrients were provided through drip irrigation system (EC 1.5 dS m^{-1}, pH 5.8–6.6, Kukka-superex N-P-K 10–5–25, Kekkilä-BVB, Vantaa, Finland) until the end of the experiment. No nutrient deficiencies were observed during the experiment (Fig. S1C). Seven, 11, and 21 after SOE, the light intensity was raised to 450, 500 and 550 μmol $m^{-2}s^{-1}$, respectively. Light intensity was measured between 380 and 780 nm with a hand-held spectrometer at canopy height (UPRTek MK350S, Zhunan township, Taiwan) and adjusted manually by dimmers attached to each luminaire. A blackout screen was deployed continuously in the greenhouse compartment throughout the experiment from taking of the cuttings until harvest to exclude outdoor radiation and to maintain the desired photoperiods. The daily light integrals (DLI) calculated from the total radiation range (380–780 nm) during propagation, vegetative phase, and at the final intensity level at flowering phase were 9.7, 22.7, and 23.8 mol $m^{-2}day^{-1}$, respectively. DLIs

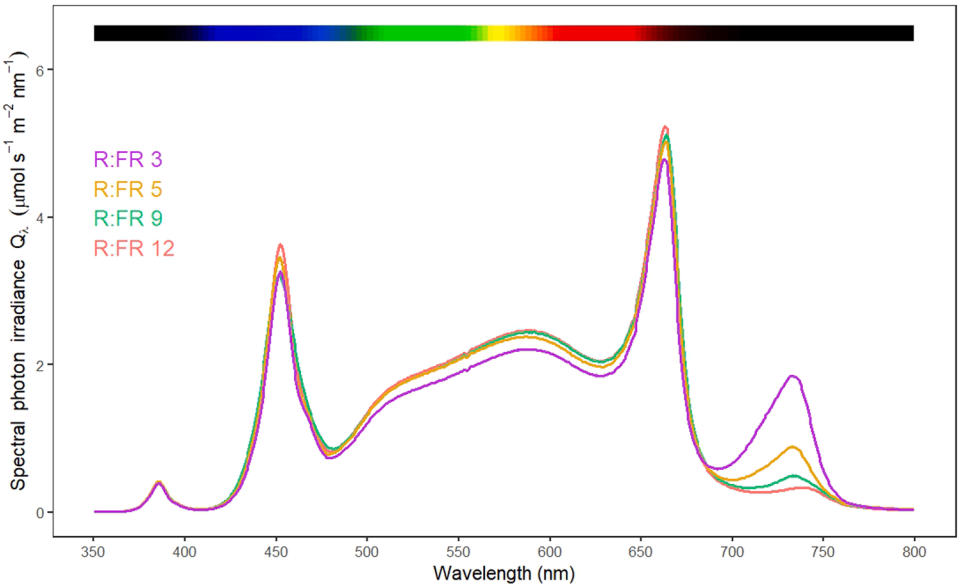

Fig. 1. The spectra of the four light treatments with different R:FR ratios (R:FR 3, 5, 9, 12) in photon quantum (Q) measured between 350 and 800 nm.

Table 1
The spectral distributions in percentages and R:FR ratios for light treatments R:FR 3, 5, 9, and 12. Ultraviolet-B (UV-B) = 280– 315 nm, ultraviolet-A (UV-A) = 315–400 nm, blue = 400–500 nm, green = 500–600 nm, red = 600–700 nm, FR = 700–780 nm, photosynthetically active radiation (PAR) = 400–700 nm. Wavelength areas for UV-B and UV-B were defined according to ISO (2007), R:FR ratio was calculated according to Sellaro et al. (2010), where red = 650–670 and FR = 720–740 nm, and fraction of FR (FR/R+FR) according to Kusuma and Bugbee (2021) where red = 650–670 nm and FR = 720–740 nm.

Treatment	UV-B %	UV-A %	Blue %	Green %	Red %	FR %	R:FR	PAR %	FR/R+FR	B:G	R:B
R:FR 3	0.02 ± 0.02	0.91 ± 0.04	17.8 ± 0.4	32.8 ± 0.5	37.0 ± 0.4	11.3 ± 1.2	2.7 ± 0.3	87.6 ± 1.2	0.06	0.75	0.59
R:FR 5	0.005 ± 0.001	0.97 ± 0.04	18.9 ± 0.3	34.9 ± 0.4	38.7 ± 0.2	6.24 ± 0.07	5.4 ± 0.1	92.5 ± 0.2	0.09	0.75	0.59
R:FR 9	0.005 ± 0.001	1.02 ± 0.04	19.5 ± 0.1	35.5 ± 0.1	39.4 ± 0.2	4.3 ± 0.3	8.6 ± 0.4	94.3 ± 0.4	0.16	0.74	0.58
R:FR 12	0.02 ± 0.02	0.99 ± 0.02	19.7 ± 0.2	36.2 ± 0.2	39.7 ± 0.1	3.2 ± 0.2	11.7 ± 0.3	95.5 ± 0.2	0.28	0.74	0.57

were calculated as DLI (mol m^{-2} d^{-1}) = (PFD (μmol $m^{-2}s^{-1}$) x photoperiod (s d^{-1})) / 1,000,000.

2.4. Plant morphology and gas exchange measurements

During the experiment, the height (cm) of all nine plants per replicate plot was measured weekly from the SOE until harvest, six times in total. Operational photosynthesis rate (μmol CO_2 m^{-2} s^{-1}) and stomatal conductance (mol H_2O m^{-2} s^{-1}) were measured 11 days after SOE from one fully opened and mature leaf per plant from mid canopy, from five randomly selected plants per replicate plot with a portable infrared gas analyzer (LICOR6400; Lincoln, Nebraska, USA). The performance of the leaf in the treatment conditions (incident PAR) at the time of sampling was measured by inserting the leaf inside a LICOR6400 cuvette with a transparent cover when temperature and CO_2 in the cuvette had acclimated to the surrounding greenhouse conditions. Stable measurements were taken when photosynthesis values stabilized. From each leaf, 2–4 measurements were taken from different parts of the leaf, and the mean was used in the statistical analysis.

To measure the effect of R:FR ratio on leaf size (individual leaf area cm^2), two fully opened and mature leaves per plant were randomly selected from each of the nine plants per plot 11 days after SOE. The leaf area (cm^2) for the two individual leaves per plant was measured with LI-3000C portable leaf area meter (Lincoln, Nebraska, USA) attached to a transparent belt conveyor accessory (LI-3050C, Lincoln, Nebraska, USA). At the end of the experiment, 49 days after SOE, the total leaf area per plant (cm^2) was measured with the same LI-3000C device by removing and scanning all leaves from a plant. For practical reasons, the total leaf area was not measured from five plants in all replicate plots, but measurements were conducted as follows; five plants in replicate 1, two plants in replicates 2 and 3, except no measurements in treatment R:FR 12 in replicate 3.

For dry mass analyses, leaves were removed and inflorescences trimmed by removing all inter-inflorescence leaves with scissors from five randomly selected plants per replicate plot. The leaves, stems, and side branch inflorescences were dried in a plant drying oven with forced air circulation (Memmert GmbH + Co. KG, Schwabach, Germany) at 72°C for 48 h and weighed for their dry weight (g) at moisture content 0 %. The apical inflorescences were dried in a similar plant-drying oven at 24 °C for 72 h and weighed for dry weight yield (g) at 0 % moisture content. The apical inflorescence dry weight (g) was later added to the dry weight measurements of the side branch inflorescences (g) to determine the total inflorescence yield (g $plant^{-1}$) at 0 % moisture content. The dried apical inflorescences were stored in a freezer (-20 °C) until measured for their cannabinoid, terpene, and flavonoid concentrations (mg g^{-1}). Dry matter partitioning within a plant was determined by calculating the fraction (%) of stem, leaves, and inflorescences from the total dry mass (g) per plant.

2.5. Cannabinoid, terpene, and flavonoid measurements from apical inflorescences

Five randomly selected plants per replicate plot were analyzed for their cannabinoid, terpene, and cannflavin A concentrations, measured as mg g^{-1} of dry weight of dried inflorescence sample. From each of the five plants, the apical inflorescences were collected fresh from the experimental plants at the time of harvest (49 days after SOE). The apical inflorescences were then trimmed and immediately dried in a plant drying oven with forced air circulation (Memmert GmbH + Co. KG, Schwabach, Germany) for 72 h (24 °C) until 0 % moisture content and stored in a freezer (-20 °C) until laboratory analysis, approximately four weeks from harvest. The complete apical inflorescence, excluding the stem, was ground with an analytical mill (IKA-Werke GmbH and Co. KG, Staufen, Germany) for 10 s. From the grind, three sub-samples per apical inflorescence were prepared. For each sub-sample, ~100.0 mg of grind was used for the extraction. The sample preparation and analysis were conducted with a two-step extraction method, in which cannabinoids and flavonoids were extracted into methanol and terpenes were extracted from the remaining methanol into hexane, as described by Kotiranta et al. (2024). Cannabinoids and Cannflavin A were analyzed with HPLC method (Agilent, Santa Clara, CA, USA), where CBDA, cannabidiol (CBD), cannabidivarinic acid (CBDVA), CBGA, Δ9- THCA, tetrahydrocannabivarinic acid (THCVA), and cannflavin A were quantified by recording the chromatograms at 280 nm and by using an external standard method. Cannabinoid standards (CBDA, CBD, CBDVA, THCA, THCVA, CBGA) were from SigmaAldrich (St. Louis, MO, USA) and cannflavin A from Cayman Chemical Company (Ann Arbor, MI, USA). After the HPLC analysis, the remaining methanol not used in HPLC analysis was used for the liquid extraction of terpenes into hexane.

The mono- and sesquiterpenes were analyzed from the hexane sample with a gas-chromatogram mass-spectrometer (GC-MS) (Perkin-Elmer, Shelton, CT, USA) according to the protocol described in detail in Kotiranta et al. (2024). Terpenes (α-pinene, β-pinene, myrcene, limonene, β-caryophyllene, bergamotene, β-farnesene, α-humulene, and β-selinene) were identified and quantified based on their mass spectra by utilizing the National Institute of Standards and Technology (NIST) Mass Spectral library, reference compounds (myrcene, β-caryophyllene, α-humulene) (SigmaAldrich, St. Louis, MO, USA)), and literature (Booth et al., 2017). The mean of the three sub-samples per apical inflorescence was used for data analysis.

2.6. Leaf flavonoid index and chlorophyll concentration

To examine the potential correlation between the floral PSM and leaf flavonoid index (LFI) prior to harvest, LFI was measured weekly with Dualex Scientific (FORCE-A, Orsay, France) from SOE until harvest, total of eight times during the experiment. Dualex Scientific device measures the leaf adaxial epidermis absorbance at λ= 375 nm where the absorbance value correlates with the leaf total flavonoid concentration (Julkunen-Tiitto et al., 2015). Leaf chlorophyll concentration (μg cm^{-2}) was measured with the same device simultaneously with flavonoid measurements to compare the relationship between leaf chlorophyll concentration, photosynthetic efficiency, and inflorescence yield. Each measuring time, three fully expanded leaves per plant were measured and the mean of the three measurements was used in the statistical analysis.

2.7. Data analysis

Data were tested for normality with the Shapiro-Wilk test prior to the analysis of variance (ANOVA) and regression analysis. The morphological traits data (dry weight of stem (g), leaves (g), apical inflorescence yield (g), side branch inflorescence yield (g), total inflorescence yield (apical + side branch inflorescence yield) (g), individual leaf area (cm^2), and total leaf area per plant (cm^2)), floral PSM concentration (mg g^{-1} dry weight) (CBGA, CBDA, THCVA, THCA, CBDVA, Cannflavin A, sum of all measured cannabinoids, cannabinoid yield per plant (sum of all measured cannabinoids (mg g^{-1}) x total inflorescence yield (g)), α-pinene, β-pinene, myrcene, limonene, β-caryophyllene, bergamotene, β-farnesene, α-humulene, and β-selinene, sum of all measured monoterpenes, sum of all measured sesquiterpenes, and sum of all measured terpenes) data were analyzed with mixed effects ANOVA model, where the fixed and random effects were light treatment and replicate block, respectively. The mean of the five plants per replicate plot (n = 3) and a significance level of $p < 0.05$ to indicate significant differences between light treatment means was used in the analyses. For repeated measurements (plant height (cm), leaf chlorophyll concentration (μg cm^{-2}), and LFI) repeated measures ANOVAs were conducted to compare the means between measuring time and the interaction between measuring time and treatments. In case the interaction result was significant ($p < 0.05$) ANOVAs were performed to examine the differences between treatment means in each measuring day. In all data analysis a Tukey's post-hoc test was performed if the ANOVA showed significant treatment effects ($p < 0.05$). LUE (g mol^{-1}) was calculated by dividing the total inflorescence yield (g m^{-2}) with the total light integral (mol m^{-2}) calculated between 380–780 nm (total irradiation) or 400–700 nm (PAR) that the plants received from SOE until harvest.

Regression analyses between the variables and R:FR ratio were conducted with treatment means to estimate the effect of R:FR on the dependent variable. The dependent variables included the apical, side branch, or the total inflorescence yield (g), leaves or stem dry weight (g), individual leaf area (cm^2), total leaf area per plant(cm^2), plant total biomass, the photosynthesis (μmol CO_2 m^{-2} s^{-1}) or stomatal conductance rate (mol H_2O m^{-2} s^{-1}), the concentrations of individual cannabinoids and terpenes (mg g^{-1}), the sum of all cannabinoids, monoterpene or sesquiterpene concentrations (mg g^{-1} dry weight), and the total cannabinoid yield (g $plant^{-1}$). The independent variable was the mean of the measured R:FR per treatment.

A comparison of the tested (linear, quadratic, logarithmic) models was performed; the model with the highest R^2 value and lowest p-value is shown in the Figs. 4–6 or the Table 2. The results which were non-significant ($p > 0.05$) in both regression and in ANOVA analyses are presented in Table 2. Significant regressions or ANOVA results are presented in Figs. 4–6 with the linear, quadratic, or logarithmic regression equation, R^2 value, and p-value and the p-value for ANOVA analysis. All data analyses were performed with SPSS 29.0.0.0 (IBM, Armonk, NY. USA).

All data are stored in Mendeley Data (Kotiranta, 2024).

3. Results

3.1. The effect of R:FR ratio on plant morphology and gas exchange

The total and the side branch inflorescence yields demonstrated a quadratic relationship with the spectrum's R:FR ratio, while the apical inflorescence yield decreased linearly with increasing R:FR ratio (Fig. 4A-C). The differences between treatment means in total, side branch, or apical inflorescence yields were small and not significant according to ANOVA (Fig. 4A-C). LUE calculated from the total irradiance (380–780 nm) had a quadratic relationship with the R:FR ratio according to the regression analysis, but no difference in treatment means was observed in the ANOVA. LUE calculated from the PAR range (400–700 nm) decreased linearly with increasing R:FR ratio according to the regression analysis, but no differences between treatment means were observed in the ANOVA (Fig. 4D). The dry weight of the stem, leaves, or total biomass, fraction of inflorescences, stem or leaves from the total biomass, individual leaf area, total leaf area, operational photosynthesis rate, or stomatal conductance rate were not affected by the R:FR ratio, nor any differences were observed between the treatment means in ANOVA (Table 2).

Difference in plant height over time was observed in the repeated measures ANOVA analysis ($p < 0.001$), as well as a significant interaction between time and light treatment ($p < 0.001$). Plant height increased under all light treatments until 29 days after SOE, after which the increase in height ceased (Fig. 2). The plants in all light treatments were equal in height at the SOE and until 14 days after SOE. From 14 days after SOE onwards, until 42 days after SOE, plants under treatment

Table 2
The regression analysis results of morphological (dry weight of total biomass, leaves, and stem, area of individual leaves, total leaf area per plant, fraction of inflorescences, stem and leaves from the total plant dry biomass), leaf gas exchange parameters (photosynthesis and stomatal conductance rate), cannabinoid concentrations (THCVA, CBDVA, and total cannabinoid yield per plant), terpene concentrations (β -pinene, β-caryophyllene, α-humulene, β-selinene, sum of all measured sesquiterpenes, sum of all measured monoterpenes, and sum of all measured terpenes) as dependent variable and treatment's R:FR ratio as independent variable and the p-values of the ANOVA test between treatment means with R:FR ratio as fixed factor and replicate as random factor. n = 3.

Parameter	Unit	Regression equation	R2	p-value (regr.)	p-value (ANOVA)
Total biomass	g	$y = -0.2x + 57$	0.208	0.543	0.687
Leaves	g	$y = 2.7\ln(x) - 0.3$	0.692	0.308	0.637
Stem	g	$y = 2.35\ln(x) - 0.08$	0.470	0.530	0.881
Individual leaf area	cm^2	$y = -0.17x + 32.5$	0.609	0.219	0.267
Total leaf area	cm^2	$y = 23.04x + 3497.8$	0.852	0.148	0.259
Fraction of inflorescences	%	$y = -0.0084x + 0.572$	0.767	0.124	0.227
Fraction of leaves	%	$y = 0.012\ln(x) + 0.2551$	0.721	0.145	0.716
Fraction of stem	%	$y = 0.002x^2 - 0.006x + 0.186$	0.870	0.360	0.514
Photosynthesis	μmol CO_2 m^{-2} s^{-1}	$y = 132 + 0.6x - 0.04x^2$	0.834	0.552	0.248
Stomatal conductance	mol H_2O m^{-2} s^{-1}	$y = 0.898 - 0.027x + 0.0019x^2$	0.999	0.052	0.908
THCVA	mg g^{-1}	$y = 0.0091\ln(x) - 0.15x$	0.886	0.059	0.133
CBDVA	mg g^{-1}	$y = 0.00105x + 0.3$	0.911	0.089	0.913
Total cannabinoid yield	g $plant^{-1}$	$y = -0.029\ln(x) + 1.6477$	0.992	0.126	0.586
β-pinene	mg g^{-1}	$y = 0.1317\ln(x) + 1.6021$	0.804	0.103	0.076
β-caryophyllene	mg g^{-1}	$y = -0.0625x + 5.8794$	0.814	0.186	0.862
α-humulene	mg g^{-1}	$y = -0.0205x + 2.4035$	0.792	0.207	0.933
β-selinene	mg g^{-1}	$y = 0.0086x + 0.43$	0.609	0.220	0.702
Sum of all measured sesquiterpenes	mg g^{-1}	$y = -0.14\ln(x) + 9.76$	0.625	0.375	0.795
Sum of all measured monoterpenes	mg g^{-1}	$y = 1.73\ln(x) + 36.10$	0.782	0.218	0.054
Sum of all measured terpenes	mg g^{-1}	$y = -32.3\ln(x) - 2.5$	7.55	0.245	0.167

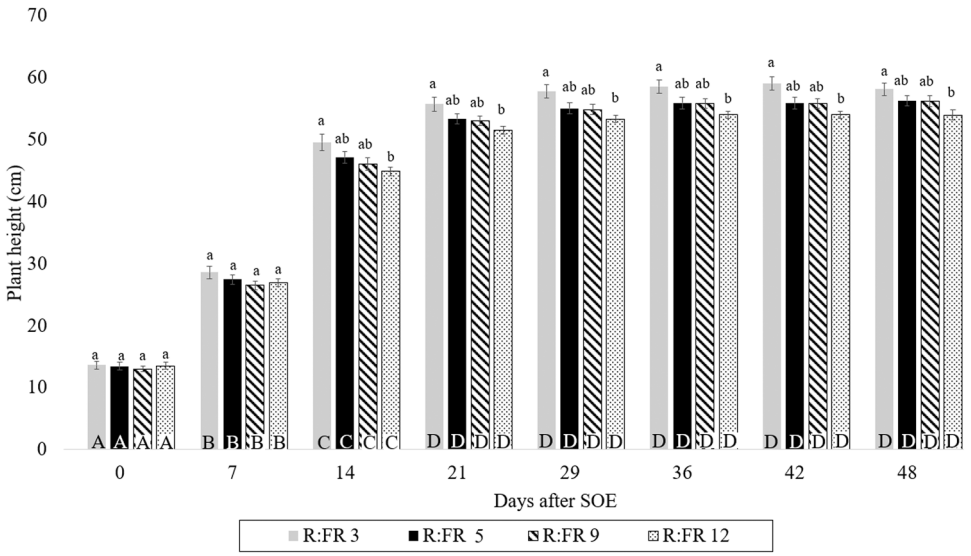

Fig. 2. Plant height of *Cannabis sativa* grown for 49 days under LED light treatments with differing R:FR ratios (R:FR 3, 5, 9, and 12) in 12 h/12 h photoperiod regime (PFD 550 μmol $m^{-2}s^{-1}$). SOE = starting of the experiment. Data are means of three replicates (± SE) each with five plants. Lower case letters above the bars indicate significant differences between treatments on the measuring day at $p < 0.05$ in Tukey's test. Upper case letters indicate significant differences within each treatment between measuring dates at $p < 0.05$.

Fig. 3. Plant morphology under four light treatments with differing R:FR ratios (R:FR 3, 5, 9, 12), PFD 550 μmol $m^{-2}s^{-1}$. Pictures were taken 42 days after starting of the experiment. White mark above the plants indicates 100 cm height measured from the bottom of the pot.

R:FR 3 were significantly taller compared to treatment R:FR 12, while plant height in treatments R:FR 5 and 9 did not differ significantly from the other treatments during the experiment. (Fig. 2 and Fig. 3).

3.2. Inflorescence cannabinoid, flavonoid, and terpene concentrations

The concentration sum of all measured cannabinoids (mg g^{-1}) was lowest in treatment R:FR 3, with no significant differences observed between the other treatments according to ANOVA (Fig. 5A). Among the measured cannabinoids and flavonoids, the concentrations of CBDA and CBGA were lower in treatment R:FR 3 compared to treatments R:FR 9 and 12 (Fig. 5B-C), THCA concentration was lower in treatment R:FR 3 compared to R:FR 5 and 12 (Fig. 5D) and the concentration of the floral flavonoid, cannflavin A, was lowest in treatment R:FR 3 (Fig. 5E), according to ANOVA. Additionally, CBDA, CBGA, and cannflavin A showed positive logarithmic correlations with the spectrum's R:FR ratio (Fig. 5B, C, E). No difference between treatment means or a relation between cannabinoid yield (g $plant^{-1}$) and R:FR was observed in ANOVA or regression analysis (Table 2).

The total terpene, monoterpene, or sesquiterpene concentrations (mg g^{-1}), calculated as the sum of the measured terpenes in the respective category, did not correlate with the R:FR ratio and no differences between the treatment means were observed in the ANOVA (Table 2). Although no difference between the treatment means in the sum of all measured monoterpenes (mg g^{-1}) was found ($p = 0.054$), the concentration of monoterpene α-pinene had a quadratic relationship with R:FR ratio, and the concentrations of monoterpenes, myrcene and limonene, were lower in treatment R:FR 3 compared to R:FR 5 according to ANOVA (Fig. 6A-C). From the individual sesquiterpenes, bergamotene and β-farnesene increased with increasing R:FR ratio according to

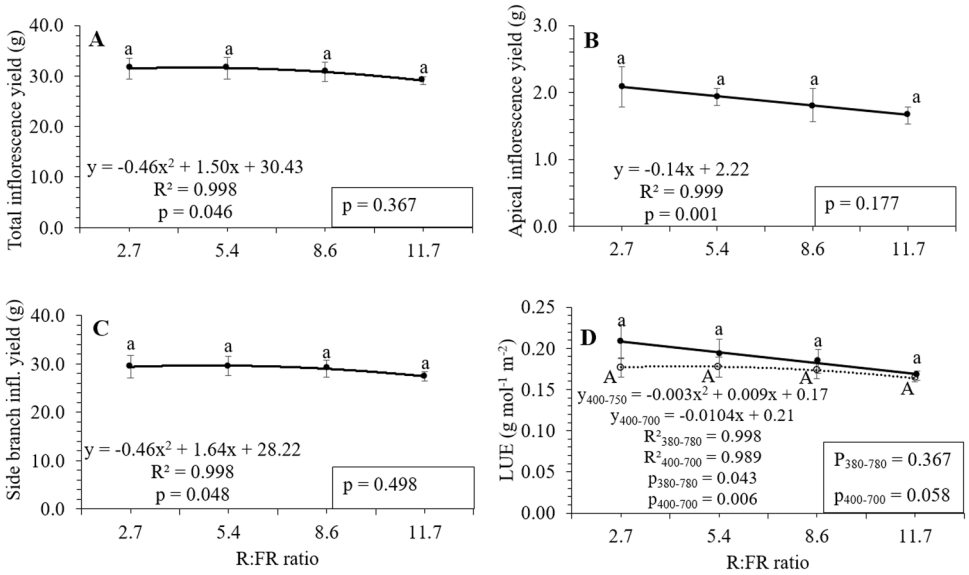

Fig. 4. The response of *C. sativa* A) total inflorescence yield (g), B) apical inflorescence yield (g), C) side branch inflorescence yield (g) and D) light use efficiency (LUE) (g mol^{-1} m^{-2}) calculated with the total radiation sum between 380–780 nm (dashed line) or with radiation sum in PAR range (400–700 nm) (solid line) to different R:FR ratios. Plants were grown under four different R:FR treatments (R:FR 3, 5, 9, and 12) for 49 days in 12 h/12 h photoperiod regime (PFD 550 µmol $m^{-2}s^{-1}$). Data are means of three replicates (± SE) each with five plants. Different lower- or upper-case letters between symbols represent a significant difference between treatment means ($p < 0.05$); the p-value from the comparison between means (ANOVA) is presented in the lower right corner in the corresponding figure. Significant linear and quadratic regression analysis results are presented with solid or dashed lines. The regression equation, R^2 -value, and p-value for the significant regression analysis are presented in the figure.

regression analyses (Fig. 6D-E), but differences between treatment means were small and not significant according to ANOVA. The concentration of β-caryophyllene, α-humulene, and β-selinene had no relation with the R:FR ratio and no differences in treatment means were observed (Table 2).

3.3. Leaf chlorophyll concentration and flavonoid content

Leaf chlorophyll concentration and LFI were measured weekly from fully developed leaves. Chlorophyll concentrations differed between measuring days ($p < 0.001$) and an interaction between time and treatment was detected ($p = 0.048$). In general, leaf chlorophyll concentrations were lower in the beginning (0–7 days after SOE) and on the last measuring day (48 days after SOE) (Fig. 7A). Leaf chlorophyll concentration was lowest in treatment R:FR 3 from 14 days after SOE until 42 days after SOE, while the highest concentrations were measured under the treatments R:FR 9 or 12 on most measuring days (Fig. 7A). In LFI a difference between measuring days was detected ($p < 0.001$) but the interaction between measuring time and light treatment was not significant ($p = 0.758$) (Fig. 7B). The maximum LFI values were reached 29 days after SOE and the values were lowest on the last measuring day (48 days after SOE) (Fig. 7B).

4. Discussion

4.1. Increasing inflorescence yield and plant height with decreasing R:FR ratio

The apical and total inflorescence yield decreased with the increasing R:FR ratio according to the regression analysis. Factors affecting yield via light spectrum can be related to photosynthesis rate (Jiang et al., 2018; Liu and van Iersel, 2023), LUE (Jin et al., 2021; Liu and van Iersel, 2023), leaf area (Liu and van Iersel, 2023), leaf chlorophyll content (Fleischer et al., 1935), or dry mass partitioning between different plant parts (Ji et al., 2020).

The link between photosynthesis rate and inflorescence yield in *C. sativa* under different light spectra has been recently studied in Jenkins (2021), Reichel et al. (2021), Danziger and Bernstein (2021a), and Holweg et al. (2024). Jenkins (2021) study concentrated on UV and blue wavelengths and found that photosynthesis, stomatal conductance, and transpiration rates were unaffected by the changes in short wavelength radiation in two out of the three tested *C. sativa* varieties, while Holweg et al. (2024) demonstrated that the addition of red (660 nm) and green radiation increased operational photosynthesis, indicating that light spectrum in general may impact the photosynthesis efficiency of *C. sativa*.

Danziger and Bernstein (2021a) and Reichel et al. (2021) had treatments containing far-red, however, the results on photosynthesis rate were inconsistent between the tested genotypes (Danziger and Bernstein, 2021a) and the spectra treatments varied also in other wavelengths besides far-red making the interpretations of the results inconclusive. In Danziger and Bernstein (2021a), treatments with the highest photosynthesis rates resulted in the highest inflorescence yields, in two out of the tested three genotypes, but did not seem to have a relation with the treatments' R:FR ratio. In Reichel et al. (2021) the treatment with the lowest R:FR ratio resulted in the highest photosynthesis rate but the lowest inflorescence yield indicating that photosynthesis rate would not be a reliable parameter to predict yield. This can also be concluded from our results, as the operational photosynthesis rate measured under the treatment conditions did not have a relation with the R:FR ratio, while the inflorescence yield did.

Before this study, the effect of far-red on photosynthesis with spectra differing only in their far-red content has not been published with *C. sativa*, but studies with other species are available. When far-red has been applied as an addition to PAR, it has been shown to increase photosynthesis rate in lettuce (Zhen and van Iersel, 2017), but when included into the total radiation by substituting PAR with far-red, the photons from PAR and far-red regions have been shown to be equal in driving photosynthesis according to Zhen and Bugbee (2020a,b). The study by Zhen and Bugbee (2020b) demonstrated that substituting varying proportions of PAR (10–40 %) with far-red light resulted in similar photosynthesis rates across 14 different species. Our results support the findings of Zhen and Bugbee (2020a,b), as no significant difference between treatments in operational photosynthesis was

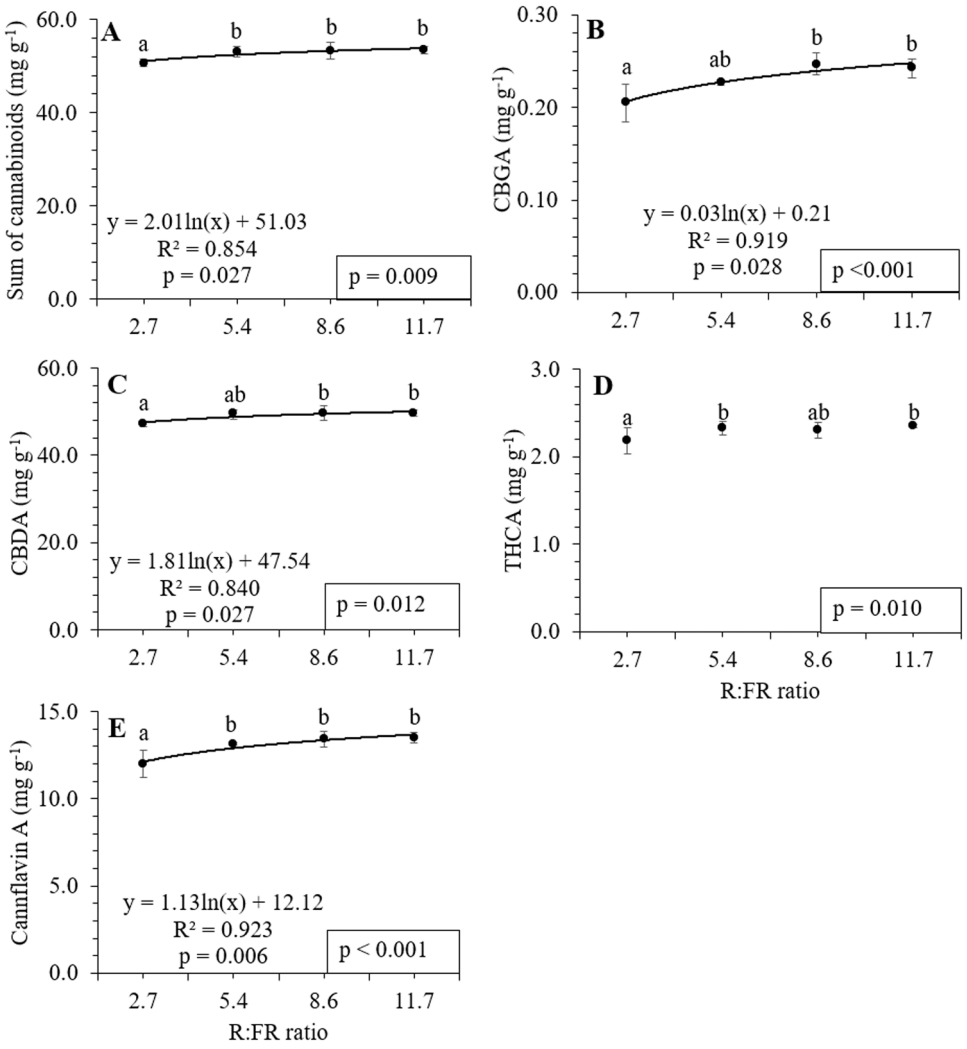

Fig. 5. The response of *C. sativa* A) sum of measured cannabinoids (mg^{-1} g^{-1}), B) inflorescence CBGA, C) CBDA, D) THCA, and E) cannflavin A concentrations ($mg^{-1}g^{-1}$) to different R:FR ratios. Plants were grown under four different R:FR treatments (R:FR 3, 5, 9, and 12) for 49 days in 12 h/12 photoperiod regime (PFD 550 μmol $m^{-2}s^{-1}$). Data are means of three replicates (± SE) each with five plants. Different letters between symbols represent a significant difference between means ($p < 0.05$); the p-value from the ANOVA is presented in the lower right corner the corresponding figure. Significant logarithmic regression analysis results are presented with solid lines, while non-significant regression analysis results are not shown. The regression equation, R^2 -value, and p-value for regression analysis are presented in the figure.

recorded when the far-red fraction of the spectrum varied between 3.2 % and 11.3 %.

It has been demonstrated that far-red radiation increases the leaf area in cucumber seedlings (Li et al., 2024), and photon capture, LUE, and harvestable yield in lettuce (Jin et al., 2021). In our study, LUEs calculated between 400–700 nm and 380–780 nm had linear and quadratic relation with the treatments' R:FR ratio, respectively, showing, that the photons were better transferred into harvestable yield in treatments with more far-red. This result aligns with the findings of Jin et al. (2021), which showed that the LUE in lettuce significantly increased with the addition of far-red light, whether calculated from the 400–700 nm or 400–800 nm wavelength range. Although increased LUE is often associated with increased leaf area and therefore better photon capture under lowered R:FR ratio (Jin et al., 2020), in this study the differences in individual or total leaf area were not affected by the R:FR ratio. It is however possible, that the leaves under the low R:FR ratio were larger and could capture more photons, even though the individual leaf area or total leaf area per plant data did not support this hypothesis. The individual leaf area was measured only once during the experiment from two leaves per plant, 11 days after SOE, thus it is possible that the timing of the measurement was not optimal to capture possible differences in leaf size. The total leaf area measurements were conducted at harvest (49 SOE), and it cannot be ruled out, that some leaves were already fallen off due to maturing.

Leaf chlorophyll concentration measurements have been considered a useful tool to indicate the photosynthesis rate potential, plant overall condition, and plant nitrate status (Fleischer, 1935) and therefore predict yield. In this study, the treatment with the lowest leaf chlorophyll concentration, R:FR 3, did not have the lowest photosynthesis rate nor the lowest inflorescence yield. In fact, while inflorescence yield decreased with increasing R:FR ratio, the chlorophyll concentration increased with increasing R:FR ratio, indicating that a direct link between chlorophyll concentration and harvestable yield should not be made.

Literature shows that plants change their dry mass partitioning between leaves, stem, and roots according to the prevailing R:FR ratio (Maliakal et al., 1999). By altering and steering the partitioning towards the reproductive parts with the spectrum's R:FR ratio, a possible yield increase in crops where seeds, inflorescences, or fruits are the harvestable yield, could be achieved as shown with tomato (Ji et al., 2020; Kalaitzoglu et al., 2019; Vincenzi et al., 2024). In this study, the differences in total inflorescence yield between treatments were small and

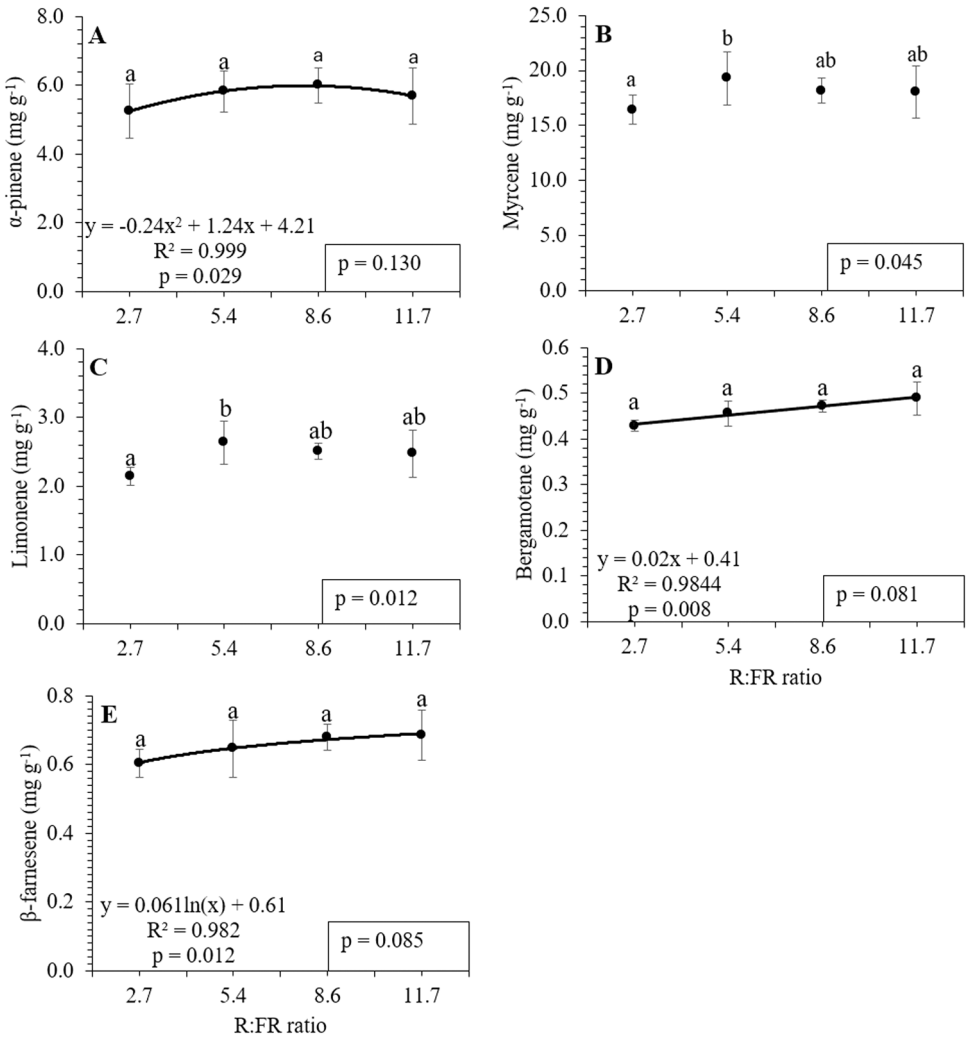

Fig. 6. The response of *C. sativa* A) α-pinene, B) myrcene, C) limonene D) bergamotene, and E) β -farnesene concentrations (mg g^{-1}) to different R:FR ratios. Plants were grown under four different R:FR treatments (R:FR 3, 5, 9, and 12) for 49 days in 12 h/12 h photoperiod regime (PFD 550 μmol m^{-2} s^{-1}). Data are means of three replicates (± SE) each with five plants. Different letters between symbols represent a significant difference between means ($p < 0.05$); the p-value from the comparison between means (ANOVA) is presented in the lower right corner the corresponding figure. Significant linear, quadratic, or logarithmic regression analysis are presented with solid lines, while non-significant regression analysis results are not shown. The regression equation, R^2 -value, and p-value for regression analysis are presented in the figure.

therefore a significant difference in dry mass partitioning, measured as fractions of leaves, stem, and inflorescences from the total dry mass was not detectable. Thus, the hypothesis of plants partitioning more dry mass to the reproductive parts under lower R:FR ratio was not supported by the regression nor ANOVA analyses. Our findings contradict those of Ji et al. (2020), Kalaitzoglu et al. (2019), and Vincenzi et al. (2024), who reported that the addition of far-red increased tomato yield and concluded that far-red enhances dry mass partitioning towards the reproductive parts. The difference between this and the above-mentioned studies lies in the composition of the light treatments. In this study, the total radiation was kept equal across treatments, whereas in the referenced studies, far-red was added on top of PAR, increasing the total radiation by 47 %, 75 %, and 26 %, respectively. It is possible that the yield increases of 13 %, 59 %, and 11 %, respectively, observed under the far-red treatments in those studies were partially a result of the increase in total radiation rather than the far-red itself.

Even though a decrease in R:FR ratio increased LUE and total and apical inflorescence yield, the differences between treatments were small, and it can be argued if using far-red would be economically feasible for a slight yield increase or larger apical inflorescences. The efficiency of far-red diodes is smaller than that of red diodes and luminaire efficacy has been shown to be more important than spectrum mediated yield increases, when looking at the production efficiency in terms of money used per produced gram of inflorescence (Westmoreland et al., 2021).

R:FR ratio affected plant morphology, and plants in the treatment with the lowest R:FR ratio (R:FR 3) were the tallest compared to the other R:FR treatments. This result is important when plant height needs to be restricted or enhanced. For example, compact plants are easier to move between locations whilst longer internodes offer a beneficial architecture for taking and planting of cuttings. In this study, the plants reached the maximum height at the same time (21 after SOE) in all treatments after which the height did not increase. It can be concluded that plant height manipulation with the light spectrum's R:FR ratio should take place prior to or during early flowering phase as the plant growth was unaffected by the spectrum's R:FR ratio after 21 days in the 12 h/12 h flowering photoperiod regime. Similar growth pattern has been observed in other light spectra studies conducted with *C. sativa* where the final plant height has been dependent on the light spectrum; however, regardless of the spectrum treatment, plants cease growth simultaneously in time (Danziger and Bernstein, 2021a; Reichel et al., 2021; Kotiranta et al., 2024). The studies by Danziger and Bernstein

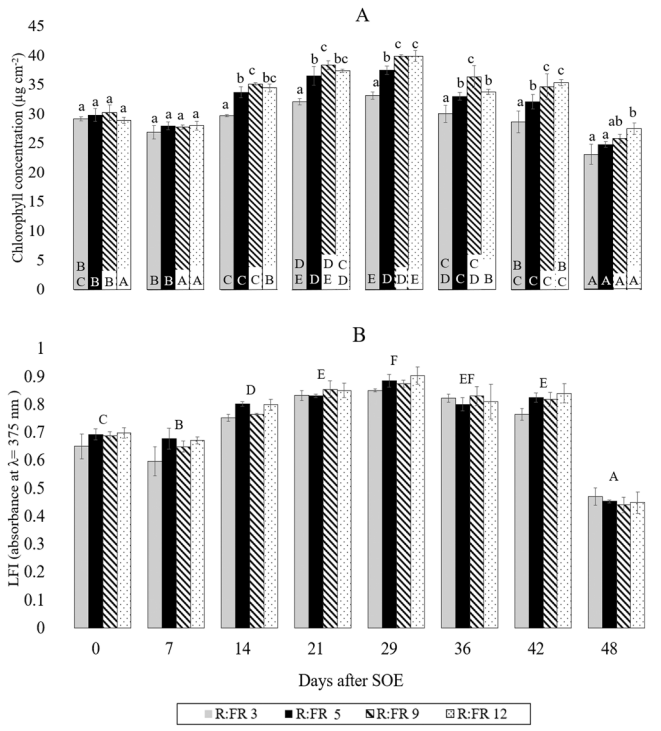

Fig. 7. Leaf chlorophyll concentration (A) and leaf flavonoid index (LFI) (B) of *C. sativa* plants grown for 48 days under LED light treatments with differing R:FR ratios (3, 5, 9, and 12) in 12 h / 12 h photoperiod regime (PFD 550 µmol $m^{-2}s^{-1}$). Data are means of three replicates (± SE) each with five plants. Lower case letters above the bars indicate significant differences between treatments on the measuring day at $p < 0.05$ in Tukey's test and upper-case letters inside bars indicate significant differences within a treatment between measuring dates at $p < 0.05$ (A). Upper case letters above bars indicate significant differences between measuring dates.

(2021a) and Reichel et al. (2021) demonstrated that the time to reach the maximum height was also dependent on the genotype and therefore an exact guideline for pre-flower or early flowering spectral treatments for height manipulation can be difficult to determine.

4.2. Terpene and cannabinoid concentrations increased with increasing R:FR ratio

While apical and total inflorescence yield decreased with increasing R:FR, the floral PSM concentrations increased with increasing R:FR ratio. The effect of far-red or spectrum's R:FR ratio on cannabinoid and terpene concentrations with spectra treatments differing only in their far-red content has been previously studied only in Kotiranta et al. (2024), where the concentrations CBD, THCVA, CBGA, all monoterpenes and a sesquiterpene, β-farnesene, decreased under the low R:FR (R:FR 1) treatment. It can be speculated, whether the differences in PSM concentrations seen in the Kotiranta et al. (2024) were solely due to the spectrum's R:FR ratio, as yield was also decreased by 68 %, indicating that the plants performed very differently in general. In this study, the concentrations of the main cannabinoids (CBDA, THCA, CBGA), and the sum of all measured cannabinoids were lowest in the lowest R:FR treatment (R:FR 3) and the concentrations of three out of four monoterpenes and two out of five sesquiterpenes increased with increasing R:FR ratio according to ANOVA or regression analyses or both. Therefore, it can be concluded that the spectrum, and more specifically, the R:FR ratio has an impact on the PSM concentrations of *C. sativa*. It can also be concluded that the spectrum, not the plant condition affected the PSM results, as flower yield increased with decreasing R:FR ratio.

In an early study conducted with thyme (*Thymus vulgaris* L.) the role of phytochromes in monoterpene production was demonstrated for the first time, when red light was shown to promote the number of trichomes and monoterpene concentrations and the response could be reversed with far-red light (Tanaka et al., 1989). In a more recent study by Kegge et al. (2013) the emission of several volatile organic compounds (VOCs), including terpenes, was demonstrated to decrease under low R:FR conditions in *Arabidopsis thaliana*. Many of the VOCs, including monoterpenes, have been linked to the plant defense system against plant pathogens and herbivores (Baldwin et al., 1997), similarly as cannabinoids have been shown to function in defense against chewing herbivores in *C. sativa* (Stack et al., 2023). In nature, a low R:FR ratio signals to plants that they are being shaded by other plants. Under these conditions, plants need to balance their resources between dry mass accumulation and PSM biosynthesis linked to plant defense (Cargnel et al., 2014). Our results show that also *C. sativa* allocates assimilates towards the reproductive parts, especially to the apical inflorescence, and less to VOCs, such as terpenes and cannabinoids under low R:FR conditions.

The spectrum's R:FR ratio affects the phytochrome equilibrium, which affects the stability of PIFs, and therefore the MEP pathway related to cannabinoid and monoterpene biosynthesis (Chenge-Espinosa et al., 2018; Desaulniers Brousseau et al., 2021). Low R:FR cause phytochromes to shift to their inactive form, which stabilizes the PIFs suppressing the key genes in the MEP pathway preventing the biosynthesis of cannabinoids and monoterpenes. In high R:FR ratio the PIFs degrade which activates the MEP pathway by removing their suppression on key genes. From the measured sesquiterpenes, β-farnesene and bergamotene concentrations decreased with decreasing R:FR ratio. Similar results were presented in Kotiranta et al. (2024) where β-farnesene concentration decreased under low R:FR treatment, but other sesquiterpenes were unaffected by the R:FR ratio while bergamotene was not detected. Cannabinoids and monoterpenes are synthetized via the MEP pathway, while sesquiterpenes are synthesized via the mevalonate (MEV) pathway (Desaulniers Brousseau et al., 2021). Through results presented here and previously in Kotiranta et al. (2024) it is evident, that different sesquiterpenes respond differently and the MEV pathway is less affected by the spectrum's R:FR ratio compared to the MEP pathway.

The LFI was measured weekly after SOE revealing differences in LFI between measuring days but no differences between treatments, while in the study by Kotiranta et al. (2024) the LFI was significantly lower under the treatment R:FR 1 compared to R:FR 11. Although no differences in the LFI between treatments were detected in this experiment, a decrease towards harvest in all treatments was recorded, which corresponds to the LFI results published previously (Kotiranta et al., 2024). A decrease in the LFI at the end of the growing cycle could be an indicator of inflorescence maturity and the reallocation process of assimilates related to senescence (Woo et al., 2019). Linking the LFI to inflorescence maturity requires more research where cannabinoid and terpene concentration data would be collected throughout the growing period and compared to the LFI data.

4.3. Considering total irradiance and spectrum composition when studying the effect of far-red radiation on plant growth

In experiments where the effect of far-red on plants is examined, the general rule is that the irradiance level should be similar between treatments to make reliable comparisons between spectra. There are two ways of matching the irradiance level. Either having similar PAR levels between treatments where far-red has been added on top of the PAR, resulting to unequal total irradiance levels between treatments. The other way, chosen in this experiment, is to match the total irradiance (PAR + far-red) between treatments, which in turn results in unequal PAR levels, as some of the PAR is substituted with far-red. Both approaches may lead to misinterpretation of the results.

Since neither of the two approaches is conclusive, the chosen approach should be taken into consideration when reporting the results

and interpreting the outcomes. In this study, the amount of PAR in the spectrum decreased with decreasing R:FR ratio, as more far-red radiation was included into the total radiation in the expense of PAR photons, resulting in a decrease in photosynthetic photon flux density (PPFD) in the lower R:FR treatments. It is in place to contemplate whether some of the results observed in this study were solely spectrum or R:FR dependent, or whether the differences in PPFD levels had an influence.

PPFD has been shown to correlate positively with inflorescence yield in *C. sativa* (Rodriguez-Morrison et al., 2021). In this study, the response was contradictory as the total inflorescence yield had a quadratic relationship with the R:FR ratio. This can indicate that the PPFD level is not the only yield determining factor, but perhaps the total PFD, including far-red, together with the spectrum composition should be considered when discussing light intensity levels. In fact, it has even been discussed whether the definition of PAR should be redetermined; Zhen and Bugbee (2020b) suggested to extend the range from 400–700 nm to 400–750 nm to have far-red radiation included in the PAR range. In Zhen and Bugbee (2020b), the addition of far-red photons to a background spectrum increased the canopy photosynthesis of 14 species similarly as adding PAR photons, indicating that FR photons are equally important for photosynthesis when coupled together with PAR.

Finally, we suggest that the responses in PSM concentrations were spectrum rather than light intensity dependent, as the PFD was equal between all treatments. In previous studies the effects of PPFD on cannabinoid and terpene concentrations have been contradictious. In the studies by Rodriguez-Morrison et al. (2021), Llewellyn et al. (2022), and Holweg et al. (2024) the PPFD level did not have an impact on the cannabinoid or terpene concentrations, while in the study by Sae-Tang et al. (2024) light intensity and total cannabinoid and terpene concentrations were shown to have a positive correlation.

5. Conclusions

This study provides evidence that adjusting R:FR ratio in the spectrum during flowering can be a tool to modify plant morphology, enhance LUE, and modify the floral cannabinoid and terpene concentrations. For example, far-red could be used in the beginning of flowering period to increase elongation and gain plant volume and switched off at the late flowering phase to avoid any reductions in PSM concentrations. Changing the spectral composition at different phases of the flowering period could also bring potential energy savings when far-red would be switched off to increase R:FR ratio when needed. Changing the spectrum between growth phases offers opportunities but should be further studied with various genotypes.

Funding

This work was supported by the Foundation of Emil Aaltonen, Emil Aaltosen säätiö (grant # 210080 KO). The LED luminaires were provided by Valoya Oy and the peat substrate by Kekkilä-BVB.

CRediT authorship contribution statement

Titta Kotilainen: Writing – review & editing, Visualization, Supervision, Resources, Methodology, Conceptualization. **Pauliina Palonen:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Conceptualization. **Stiina Kotiranta:** Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Aku Sarka:** Writing – review & editing, Methodology, Investigation, Formal analysis.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Stiina Kotiranta reports financial support and equipment, drugs, or supplies were provided by Valoya Oy. Aku Sarka reports financial support was provided by Valoya Oy. Stiina Kotiranta reports a relationship with Valoya Oy that includes: employment. Aku Sarka reports a relationship with Valoya Oy that includes: employment. Stiina Kotiranta and Aku Sarka were employees of Valoya Oy at the time the experiments were conducted. For Stiina Kotiranta the work relationship ended in September 2022, while Aku Sarka is still currently employed by Valoya Oy. 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.

Acknowledgments

The authors would like to thank Tiina Sarja-Lambert for her contribution in the maintenance of the experimental plants and data collection. We would also like to thank the greenhouse staff at the University of Helsinki for their support and advice prior to and during the experiments, Riitta Henriksson and Juha-Matti Pihlava from the Natural Resources Institute (LUKE) for their time and guidance in the laboratory, and the Valoya Oy staff for the LED equipment and technical support during the experiments.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.envexpbot.2024.106059.

Data availability

Cannabis sativa, R:FR ratio, cannabinoids and yield (Mendeley Data)

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