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Gradually increasing light intensity during the growth period increases dry weight production compared to constant or gradually decreasing light intensity in lettuce

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ABSTRACT

The objective of this research was to investigate the effects of gradually increasing or decreasing photosynthetic photon flux density (PPFD) during cultivation compared to a constant PPFD on biomass production. Lettuce plants (*Lactuca sativa* L. 'Expertise') were grown in climate rooms in which every three days the PPFD was increased by 16 μmol m^{-2} s^{-1} (from 140 to 300 μmol m^{-2} s^{-1} from day 0 to 30), decreased (from 300 to 140 μmol m^{-2} s^{-1}), or kept constant (221 μmol m^{-2} s^{-1}), while the total light integral at the end of the cultivation period (30 d) was the same for all three treatments. Gradually increasing PPFD resulted in a 16 or 13% increase in total plant dry weight compared to treatments with decreasing or constant PPFD, respectively. This increase was explained by a higher light interception mainly because, in this treatment, most of the light was provided at the end of the cultivation period when the leaf area index was high. Consequently, the light use efficiency based on incident PPFD was highest when PPFD gradually increased, even though the light use efficiency based on intercepted PPFD was highest when PPFD gradually decreased during cultivation. Despite the higher shoot dry weight when PPFD gradually increased, shoot fresh weight was not significantly affected by the light treatments. This difference in response between fresh and dry weight resulted from a higher shoot dry matter content when PPFD gradually increased. Our results show that gradually increasing PPFD had a positive effect on dry weight accumulation and increased dry matter content, but did not affect the shelf life. So, although vertical farms enable growers to keep all conditions constant, some dynamic variation of conditions might be needed for optimizing the light use efficiency.

1. Introduction

Vertical farming is a relatively new food production system where crops are cultivated indoors and all the growing light is provided by lamps (Kozai and Niu, 2019; SharathKumar et al., 2020; van Delden et al., 2021). Vertical farms are closed systems where all environmental factors, including light, temperature, relative humidity, and CO_2 concentration, can be well-controlled, and the resources, such as water and nutrients can be fully recycled. Vertical farming scores high in water, land and nutrient use efficiency while the use of pesticides can be avoided (Van Delden et al., 2021). However, the high energy consumption is a bottleneck for further development of vertical farming. The lighting system takes up a significant amount of the total energy consumption (Van Delden et al., 2021). Similarly, in greenhouse cultivation in northern latitudes where supplementary lighting is used in winter, the lighting also leads to high energy use (e.g. Katzin et al., 2021). Thus, it is urgent to improve light use efficiency, i.e., the amount of fresh produce produced per unit of incident light.

In vertical farms and greenhouses the photosynthetic photon flux density (PPFD, 400–700 nm) of electric lighting is usually kept constant throughout the cultivation period from transplanting until harvest. However, keeping the incident PPFD constant might mean that the intensity is too high in the beginning and too low shortly before harvest. In the early growing period, when the leaf area index is still small, a large fraction of the light falls on the floor instead of being absorbed by the plants. This can lead to a relatively low light use efficiency based on

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incident light. Once the canopy is closed, the plants can intercept and utilize a larger fraction of the incident light. Therefore, a gradual increase of PPFD during the cultivation period may lead to higher biomass production and light use efficiency compared to cultivation where PPFD is kept constant throughout the cultivation cycle. However, when PPFD would gradually decrease during the cultivation period and hence a high PPFD would be provided in the initial stages of cultivation, the high light levels during early growth may promote crop growth by a faster leaf area expansion, resulting in a strong increase in plant growth as the crop grows exponentially in this period (Goudriaan and Monteith, 1990). Increasing the light interception in the early days will benefit the canopy light interception afterwards and possibly increase the final biomass production. So, there are two contrasting effects that determine the final effect of a gradual change in light intensity during the cultivation period of the crop on biomass production and light use efficiency.

In addition to the effect on biomass production, a high PPFD during the whole cultivation cycle may have a positive effect on shelf life and visual quality of leafy greens such as lettuce (Woltering and Witkowska, 2016; Min et al., 2021). In particular a high PPFD at the end of the cultivation substantially increased the shelf life of lettuce (Min et al., 2021).

Although many studies have investigated the effects of PPFD (e.g., Pennisi et al., 2020; Carotti et al., 2021), the effects of gradually changing the PPFD during the cultivation cycle, while keeping the total light sum constant have hardly been studied. The research of Yamada et al. (2000) on potato seedlings suggests that increasing the light intensity during the cultivation period can increase biomass production. The objective of this research was to investigate the effects of gradually increasing or decreasing PPFD during cultivation compared to constant average PPFD on biomass production. We hypothesised that gradually increasing PPFD will maximize the light interception, produce more total dry weight and improve light use efficiency. An experiment was conducted with lettuce in climate rooms in which every three days the daily light integral was increased, decreased, or kept constant during the cultivation period while the total light integral at the end of the cultivation was the same for all three treatments. All other growth conditions were kept constant and equal for all three treatments. Yield component analysis (Higashide and Heuvelink, 2009; Ji et al., 2019) was used to quantify the contributions of underlying components of the effects of treatments on biomass production. Also shelf life was determined.

2. Materials and methods

2.1. Plant material and growth conditions

Lettuce (*Lactuca sativa* L. cv. Expertise, Rijk Zwaan, the Netherlands) was grown in a climate room with six compartments divided by white plastic screens. Seeds were sown in stone wool plugs in 240-cell trays (Grodan, Roermond, the Netherlands). The seeds were sown in darkness at 21.5 °C (22 °C during 18 h and 20 °C during 6 h of each diel cycle. Two days after sowing, they were placed in the light (18h light/6h dark) with a PPFD of 145 ± 1.3 μmol m^{-2} s^{-1} provided by red (R) and blue (B) LEDs (88% R and 12% B) (GreenPower LED research modules, and GreenPower LED production modules, 2nd generation, Philips, the Netherlands). Seven days after sowing, plugs with seedlings having two cotyledons were transplanted to individual stone wool blocks (7 cm × 7 cm × 7 cm, L × W × H, Grodan, Roermond, the Netherlands) and were grown for 30 days at a planting density of 51 plants m^{-2}. Plants were distributed equidistantly following a chess-board pattern. Plants in the outer rows in each plot were considered border plants and not used for measurements. After each destructive harvest plants were relocated to keep the original planting density.

The stone wool blocks were always in a 1.0–1.5 cm layer of nutrient solution. Nutrient solution (electrical conductivity (EC) 2.3 dS·m^{-1} and pH 5.8), containing 0.38 mM NH_4^+, 8.82 mM K^+, 4.22 mM Ca^{2+}, 1.15 mM Mg^{2+}, 12.92 mM NO_3^-, 1.53 mM Cl^-, 1.53 mM SO_4^{2-}, 0.12 mM HCO_3^-, 1.53 mM $H_2PO_4^-$, 0.38 mM SiO_3^{2-}, 30.67 μM Fe^{3+}, 3.83 μM Mn^{2+}, 3.83 μM Zn^{2+}, 38.33 μM B, 0.77 μM Cu^{2+} and 0.38 μM Mo, was applied from the second day after transplanting. The nutrient solution was completely renewed twice a week to keep EC, composition, and pH stable. Averages (±standard deviations) of temperature and relative humidity (RH) were 22.0 ± 0.01 °C and 74.6 ± 0.7% during the photoperiod and 19.9 ± 0.01 °C and 79.5 ± 0.5% during the dark period, respectively. CO_2 concentration was kept at 752 ± 28ppm.

2.2. Light treatments

During the 30 days growth period, the incident light contained R (600–700 nm), B (400–500 nm) and Far-Red (FR: 700–800 nm). For all treatments and repetitions, the R and B intensity ratio was kept at 7.4 ± 0.0 and the R to FR intensity ratio was kept 5.2 ± 0.1 (GreenPower LED research module, and GreenPower LED production module, 2nd generation, Philips, the Netherlands). Light treatments started on the day of transplanting. Three treatments (increasing, decreasing and constant PPFD) were applied through the 30 days cultivation period. The Increasing and Decreasing treatments were realized by stepwise increasing and decreasing incident PPFD by 16 μmol m^{-2} s^{-1} every three days (Fig. 1). Incident PPFD at canopy level was kept constant at 221 μmol m^{-2} s^{-1} throughout cultivation for the Constant treatment (Fig. 1). Incident photosynthetically photon flux density (PPFD) integral at the end of the cultivation was 428 ± 1.0, 428 ± 0.5 and 430 ± 1.8 mol m^{-2} for the Increasing, Decreasing and Constant treatments, respectively. Light measurements were performed at canopy height using a quantum sensor (LI-250A, LI-COR, Lincoln, United States) for PPFD and a spectroradiometer (SS-110, Apogee Instruments, Utah, United States) for spectrum. The average PPFD was determined at 24 locations per treatment in each repetition.

2.3. Measurement of growth parameters

Destructive measurements were conducted at 0, 6, 12, 18, 24, and 30 days after transplanting (DAT). Pictures from above the canopy were taken (iPhone 7, Apple, Cupertino, CA, USA) before destructive measurement for estimation of canopy projected leaf area at 12, 18, 24, and 30 DAT. Pictures were taken at a fixed position from the canopy with a ruler placed next to the plants. Canopy projected leaf area was extracted by using ImageJ (IOCI, University of Wisconsin-Madison, Madison, WI, USA). Leaf area was determined using a leaf area meter (LI-3100 Area Meter, Li-Cor, Lincoln, United States). Fresh and dry weights (forced air oven at 105 °C for 24 h) of shoot and root were determined. As the stem of this cultivar was extremely small, leaf dry weight was considered equal to the shoot dry weight. From 18 DAT onwards the lettuce root dry weight was determined by oven drying of the stone wool before and after the experiment; the difference was estimated to be the root dry weight. At 0, 6, and 12 DAT, when the lettuce roots were relatively small, the root dry weight was considered to be 15% of total dry weight, being the average fraction determined at 18 DAT.

The floor coverage fraction was calculated based on plant projected leaf area per plant and a planting density of 51 plant m^{-2}. The daily floor coverage fraction was calculated by linear interpolation between measurement days at 6, 12, 18, 24 and 30 DAT. The floor coverage fraction at 0 DAT was assumed to be zero while at 6 DAT it was calculated from leaf area as there was no mutual shading of leaves. Daily light interception was calculated as the product of incident PPFD at the top of the canopy and floor coverage fraction at that day.

Incident light use efficiency (LUE_{inc}) was calculated as the ratio between plant total dry weight and cumulative incident PAR (400–700 nm) at canopy level. Intercepted light use efficiency (LUE_{int}) was calculated as the ratio between plant total dry weight and cumulative intercepted PAR.

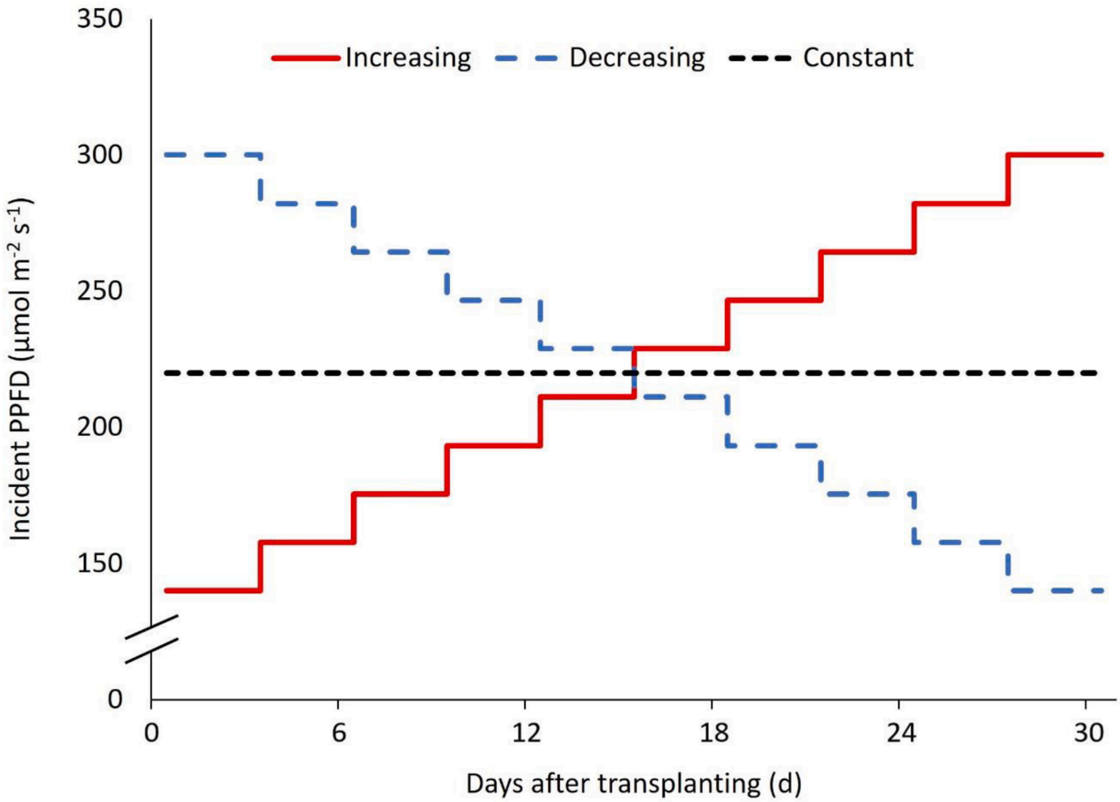

Fig. 1. Time course of the incident photosynthetic photon flux density (PPFD: 400–700 nm) during the growth period for treatments with constant, increasing, and decreasing light intensities. In all treatments the intensity averaged over the whole cultivation period was the same.

2.4. Yield component analysis

Treatment effects on fresh yield can be analysed by breaking down shoot fresh weight into underlying components (Fig. 2). In this analysis, shoot fresh weight (FW_{shoot}) is the product of shoot dry weight (DW_{shoot}) and the fresh:dry shoot weight ratio (FW_{shoot}:DW_{shoot}). Shoot dry weight is the product of total plant dry weight (DW_{plant}) and fraction of biomass partitioned to the shoot (DW_{shoot}: DW_{plant}). Total plant dry weight is the product of intercepted light use efficiency (LUE_{int}; dry weight per unit intercepted PPFD) and canopy intercepted PPFD (I_{int}). I_{int} is the cumulative PPFD interception during the whole cultivating period (0–30 DAT).

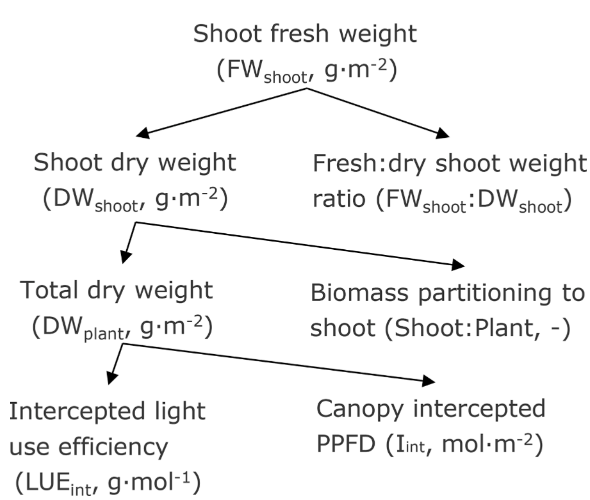

Fig. 2. Shoot fresh weight separated into underlying components. Abbreviations and units are given in between brackets.

2.5. Overall visual quality and shelf life

Overall visual quality of the lettuce was determined at final harvest (30 DAT) and after 5, 10, and 15 days of storage at 12 °C in darkness. At harvest, three lettuces were cut in squares of 2 × 2 cm and stored in two plastic boxes (18 L × 13 W × 6.5 H cm) per treatment per repetition. Two pieces of wet filter paper were placed underneath to keep the moisture in the box. In the lids, nine holes were made with a 1 mm syringe needle to avoid a build-up of CO_2. The scoring of overall visual quality was carried out according to Min et al. (2021). In brief, the evaluation of the overall visual quality was done by three assessors at room temperature. At each time point for the two boxes from each treatment and each repetition were taken out of storage and scored from 1 to 9, (i.e. 9 being the best and 1 the worst). The scoring was based on parameters such as colour change (yellowing, browning, and pinking), crispness and overall decay. The acceptance limit was set at 6; when the score fell below the limit the box had reached the end of shelf life.

2.6. Statistical setup and analysis

A randomized complete block design was applied. The experiment was repeated three times (blocks) and each time contained two repetitions representing three blocks and a total of six repetitions (n = 6). There were three sampling plants per treatment per repetition for each destructive measurement. At DAT 6, no destructive harvest was done for the 3rd block (repetition 5 and 6) and nine plants were sampled at the final harvest of this 3rd block. Overall visual quality and shelf life tests were done in block 1 and 2 (repetitions 1 to 4). For each block, new randomization of the light treatments positions was done in the climate chamber. Analysis of variance was used to determine treatment effects using Genstat software (18th edition, United Kingdom). Treatment effects were tested at α = 0.05 and assumptions for homogeneity and normality of residuals were tested with Bartlett's test and Shapiro-Wilk test, respectively and all were accepted ($P > 0.05$). Mean separation was done with Fisher's Protected LSD test ($P = 0.05$).

3. Results

3.1. Biomass production, leaf area, and dry matter content

During each 6-day period the rate of shoot dry weight growth increased with increasing PPFD of that specific period (Fig. 3a). Similarly, the rate of shoot fresh weight growth increased with increasing

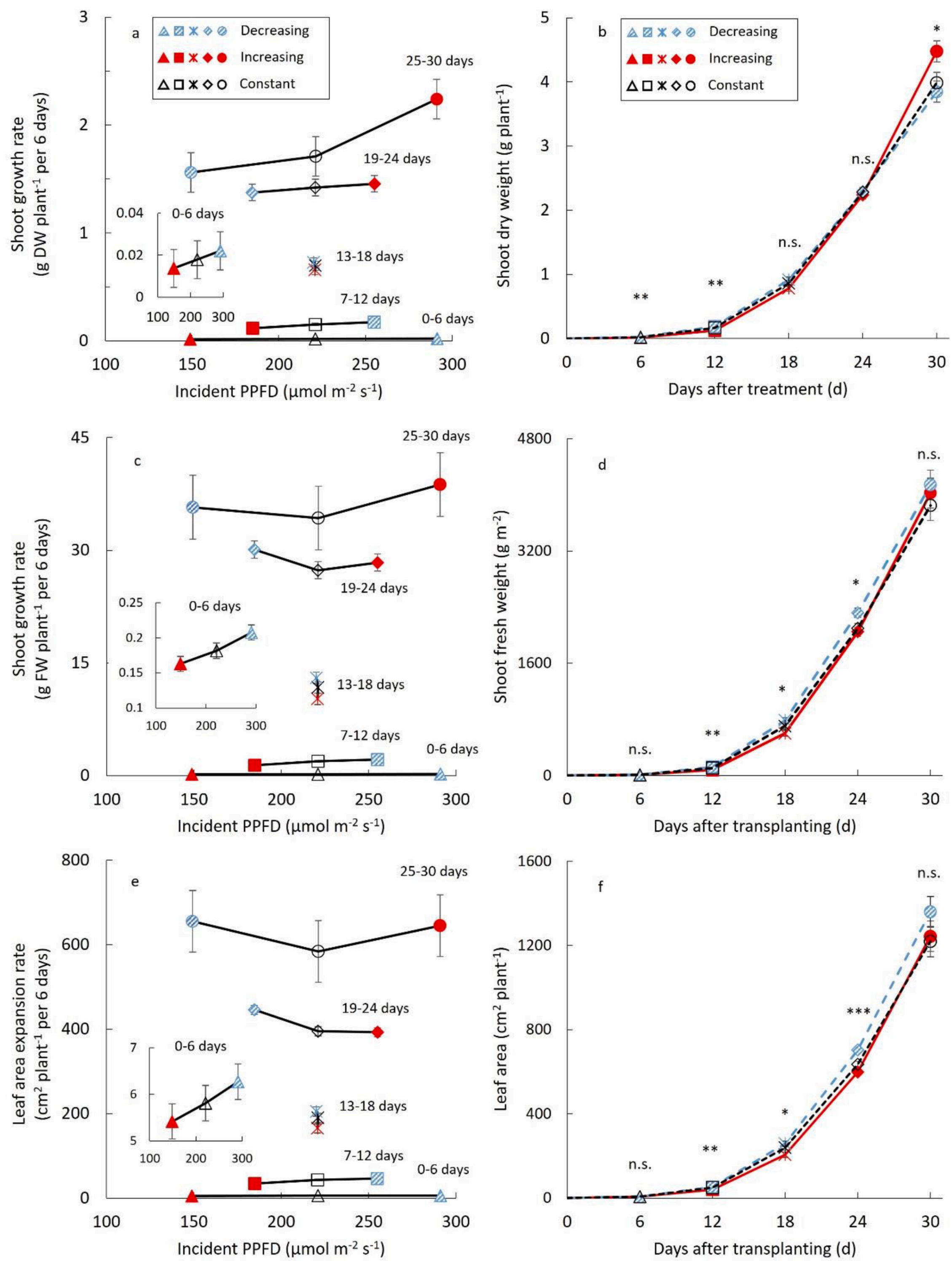

Fig. 3. The effects of constant PPFD versus gradually increasing or decreasing PPFD throughout the cultivation period on dry (a) and fresh (c) shoot growth rate, and leaf area expansion rate (e) for each 6-days sampling interval and the cumulative shoot dry weight (b), shoot fresh weight (d), and leaf area (f) at different sampling point. Data are the means of four (DAT 6; $n = 4$) or six repetitions ($n = 6$). Error bars represent standard error of means. * indicates significant effect of light treatment at $*P = 0.05$, $**P = 0.01$ and $***P = 0.001$. n.s. stands for not significant. The inset shows an enlargement of the first interval.

PPFD during the initial period of the cultivation cycle (Fig. 3c, inserted panel). However, during the last two periods of the cultivation cycle the rate of fresh weight growth was hardly affected by the PPFD. Growth rates during the later periods were much larger than during the initial periods. Therefore, the effects of the later periods on final shoot weight were largest. Consequently, whether PPFD decreased, increased or was constant during the cultivation there was no substantial difference in the final fresh weight at the end of the cultivation cycle (Fig. 3d). However, the final shoot dry weight was 16% and 13% higher when PPFD increased during cultivation, compared to decreasing and constant light treatments, respectively (Fig. 3b). The final plant dry weight (shoot+-root) was 19% and 13% higher for the increasing light treatment compared to decreasing and constant light treatments, respectively.

A higher PPFD promoted leaf area expansion rate during the initial periods (Fig. 3e, inserted panel), even though the differences were limited. However, an effect of PPFD on leaf area expansion rate was not observed during the final periods. Cumulatively, plants in decreasing light treatment had the highest leaf area during the first part of the growth cycle; at the end of the experiment leaf area seemed to be 9–12% higher than in the other two treatments, but this difference was not statistically significant anymore (Fig. 3f). The specific leaf area (SLA) decreased with an increase in PPFD of the 6-days period preceding the measurements (Fig. 4a). At the end of the experiment the decreasing light treatment had 46% larger specific leaf area (SLA) than increasing treatment. The dry matter content (DMC) decreased during cultivation while at each sampling point it increased with an increase in PPFD of the 6- day period preceding the measurements, except for the first sampling point at day 12 (Fig. 4b).

3.2. Floor coverage fraction, cumulative PPFD interception, and light use efficiency based on incident and intercepted PPFD

Even though there were significant differences in leaf area at each sampling point (Fig. 3f), there were only small differences in floor coverage fraction among treatments during growth (Fig. 5a). Assuming proportionality between floor coverage fraction and fraction light intercepted, the fraction of light intercepted differed only slightly among treatments for each specific date. Consequently, cumulative over the whole cultivation period, the increasing light treatment intercepted more PPFD than constant and decreasing light treatments (Fig. 5b), as for this light treatment a higher incident PPFD coincided with the cultivation period with high floor coverage. Correspondingly, intercepted PPFD was lowest for the decreasing light treatment, as for this treatment a low incident PPFD coincided with the period with high floor coverage.

The decreasing light treatment resulted in the highest light use efficiency (LUE) based on intercepted PPFD (ratio plant dry weight: cumulative intercepted PPFD) being 1.23 g mol^{-1}, which was 11.2% higher compared to the increasing light treatment and 10.6% higher compared to the constant light treatment (Fig. 6A). However, as the increasing light treatment intercepted most light (Fig. 5b), it had the highest LUE based on incident PPFD (ratio plant dry weight: cumulative incident PPFD). LUE based on incident PPFD was 0.62 g mol^{-1} for the increasing light treatment, which was 19% higher compared to the decreasing light treatment and 13% higher compared to the constant light treatment (Fig. 6B).

3.3. Yield component analysis

The absence of a significant effect of light treatments on the final shoot fresh weight (FW_{shoot}) (Figs. 4d and 7) was related to the contrasting effects of the light treatments on the final shoot dry weight (FW_{shoot}) and the fresh: dry weight ratio of the shoot (FW_{shoot}/DW_{shoot}). Effects of light treatments on shoot dry weight were largely due to effects on total plant dry weight as treatment effects on dry matter partitioning between shoot and root were small. Nevertheless, the 2% increase in shoot: plant ratio in the decreasing light treatment versus constant light treatment was statistically significant. The increased final plant dry weight in the increasing light treatment was associated with an increase in the cumulative amount of intercepted light (I_{int}). The decreased plant dry weight in the decreasing light treatment was associated with a lower cumulative amount of intercepted light which was partly compensated by a higher light use efficiency of intercepted light (LUE_{int}).

3.4. Overall visual quality and shelf life

At harvest all leaves were crisp and green. During storage the overall visual quality of the fresh-cut lettuce declined due to browning and pinking at cut edges and yellowing (Fig. 8). Overall visual quality at harvest and post-harvest, hence shelf life, were not significantly affected by the light treatments.

4. Discussion

4.1. Gradually increasing PPFD resulted in the highest LUE_{inc} due to the highest light interception

A gradual increase in PPFD during cultivation resulted in a higher LUE_{inc} (LUE based on incident PPFD) compared to a constant PPFD or a gradually decreasing PPFD, when total light integral over the whole cultivation period was kept the same (Fig. 6b). The main reason for this higher LUE_{inc} was the increased light interception (Fig. 5b). A gradually increasing PPFD means that the high PPFD coincides with a high fraction

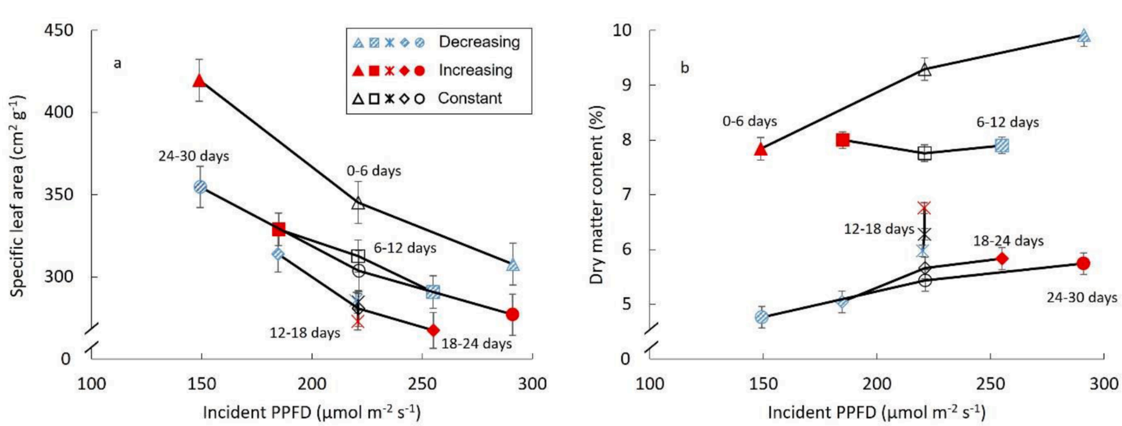

Fig. 4. The effects of constant PPFD versus gradually increasing or decreasing PPFD throughout the cultivation period on specific leaf area (a) and dry matter content (b) for each 6-days sampling interval. Data are the means of four (DAT 6; $n = 4$) or six repetitions ($n = 6$). Error bars represent standard error of means.

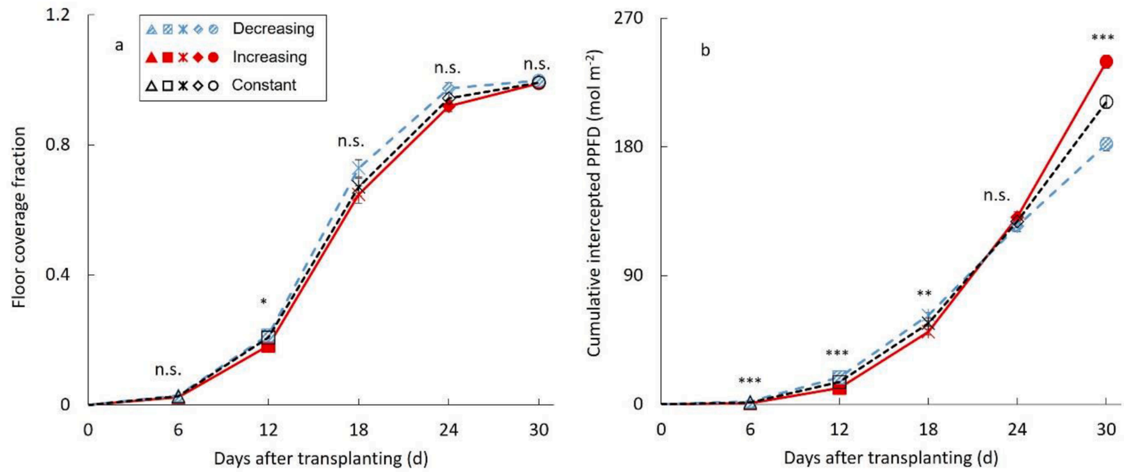

Fig. 5. Time course of the floor coverage fraction (a) and cumulative intercepted PPFD (b) when PPFD was constant PPFD, or gradually increasing or decreasing throughout the cultivation period. Data are the means of four (DAT 6; $n = 4$) or six repetitions ($n = 6$). Error bars represent standard error of means. * indicates significant effect of light treatment at $^*P = 0.05$, $^{**}P = 0.01$ and $^{***}P = 0.001$. n.s. stands for not significant.

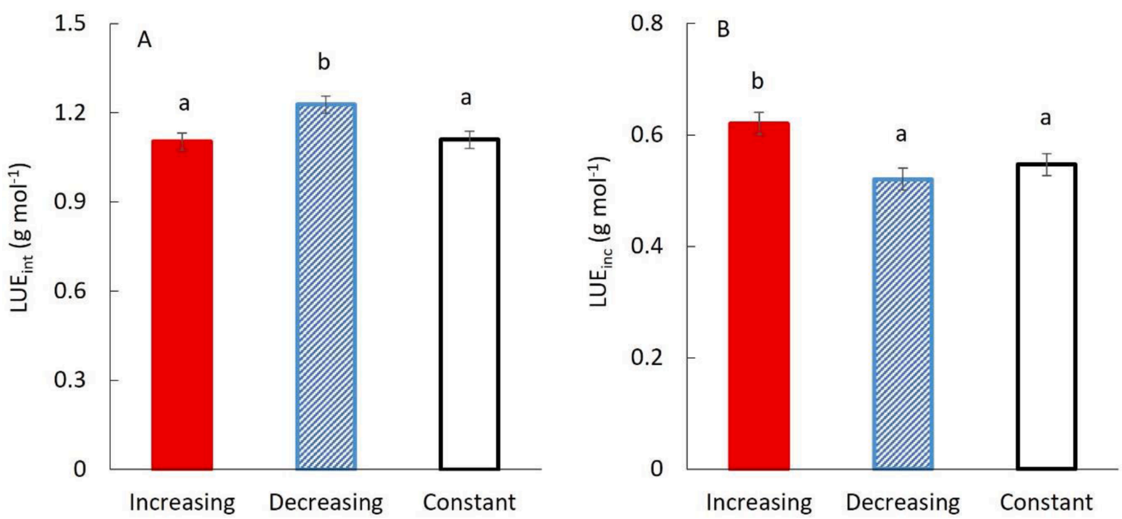

Fig. 6. (A) Intercepted light use efficiency (LUE_{in}, ratio plant dry weight: cumulative intercepted PPFD), and (B) incident light use efficiency (LUE_{inc}, ratio plant dry weight: cumulative incident PPFD) of lettuce plants grown at increasing, decreasing or constant PPFD during 30 days of cultivation. Data are the means of six repetitions ($n = 6$). Error bars indicate standard errors of means. Different letters indicate significant differences between treatments ($P < 0.01$).

of light intercepted at the end of the growing period. In the treatment with gradually decreasing PPFD, high intensities were provided when the plants were small, and consequently, a lot of light was not absorbed by plants but lost on the floor.

In line with our results, Yamada et al. (2000) grew sweet potato seedlings for 15 days under stepwise increasing light (100, 200, followed by 300 μmol m^{-2} s^{-1}) or constant PPFD (200 μmol m^{-2} s^{-1}) and concluded that the increasing light treatment produced 10% more biomass.

Specific leaf area (SLA) is an important factor contributing to light interception and light distribution in the canopy. SLA continuously acclimated to the PPFD of the preceding days, being lower the higher the PPFD (Fig. 4a). A decrease in SLA with increasing PPFD or daily light integral is in line with other studies (e.g. Poorter et al., 2019; Carotti et al., 2021; Ghorbanzadeh et al., 2021). Consequently, SLA was initially higher in the treatment with increasing PPFD, compared to constant or decreasing PPFD (Fig. 4a). In the early crop stages a large fraction of light is not intercepted by leaves. In this crop stage an increase in SLA, hence “thinner” leaves, will have resulted in a higher fraction light intercepted, when comparing at the same leaf weight, and, therefore, will have contributed to an increased LUE_{inc}. At a later stage of growth a large fraction of incident light was intercepted in all treatments (Fig. 4b) which makes that the effects of SLA on canopy photosynthesis and crop growth were probably small in this stage. In summary, low PPFD leads to high SLA. When PPFD increases during crop cultivation, plants are initially exposed to low PPFD leading to lower SLA, which is likely to increase LUE_{inc}. In the later stages difference in SLA are hardly affecting light interception, and, therefore, hardly affecting LUE_{inc}. Hence the effects of treatments on SLA in the young plants can partly explain the observed treatment effects on LUE_{inc}.

The observed effects likely depended on the planting density as well as the range of light intensities used. Here we used a relatively high planting density of 51 plants per m^2 (Jin et al., 2021). When a lower planting density had been applied, maybe a larger effect of the gradual changes in PPFD would have been observed, as with a lower planting density initially a larger fraction of light is not intercepted by the leaves. As an alternative to increasing PPFD, which increases the amount of light intercepted per plant during the cultivation, a grower with a hydroponic system might apply a strategy where he keeps PPFD constant but varies plant spacing. In the present study the intensity ranged from

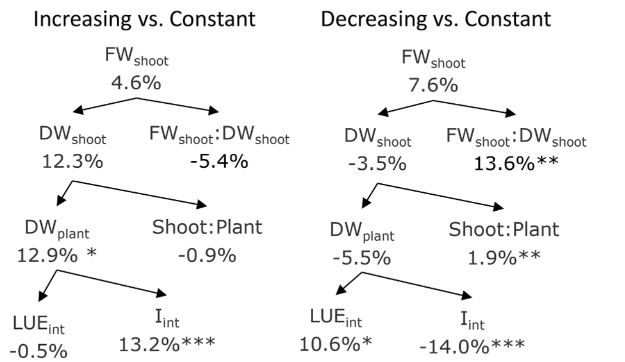

Fig. 7. Effect of gradually increasing or decreasing PPFD compared to constant PPFD during cultivation. Percentages indicate the difference between increasing and constant light treatment (left) or between decreasing and constant light increment (right). Abbreviations: FW_{shoot} (shoot fresh weight), DW_{shoot} (shoot dry weight), FW_{shoot}:DW_{shoot} (shoot fresh: dry weight ratio), DW_{plant} (plant dry weight), Shoot: Plant (fraction of shoot dry weight in total plant dry weight), LUE_{int} (intercepted light use efficiency), and I_{int} (canopy intercepted PPFD integral). * $P = 0.05$, ** $P = 0.01$ and ***$P = 0.001$. The statistical analysis was conducted based on all treatments for each parameter. Data are the means of six repetitions ($n = 6$).

140 to 300 μmol m^{-2} s^{-1}. When the range would be very small, smaller effects are expected. Likewise, when the range of light intensities would be much larger the difference in biomass between increasing and decreasing PPFD is likely to be larger. Our experiments were performed with one variety; it might be interesting to verify if similar effects would be observed with other cultivars.

4.2. Gradually decreasing PPFD resulted in the highest LUE_{int}

In contrast to LUE_{inc}, the LUE_{int} (LUE based on intercepted PPFD) was highest in the treatment where the PPFD gradually decreased during cultivation (Fig. 6). The main reason for this effect is that the LUE_{int} slightly decreased with increasing PPFD and that the LUE_{int} was highest in the later growth stages of the plants (Supplementary Fig. S1). This makes that the later growth stages have a dominating effect on the overall response of LUE_{int} to the light treatments. In the treatment with gradually decreasing PPFD, PPFD was lowest during the last growth stages and therefore also the LUE_{int} calculated over the whole cultivation cycle was highest.

Although a gradual increase in PPFD during the cultivation period resulted in the highest shoot dry weight at harvest, shoot fresh weight did not significantly differ whether PPFD was constant, decreased, or increased during cultivation (while in all cases the light integral was the same; Fig. 3d). This is in line with results of Xu et al. (2020) who varied the PPFD during the last 12 days of cultivation while keeping light integral constant and did not find an effect on final fresh weight. The difference we found in responses between fresh and dry weight was related to differences in dry matter content (ratio between dry and fresh weight). At most time points the dry matter content increased with increasing PPFD during the preceding days (Fig. 4b). This effect of PPFD on dry matter content agrees well with the finding of Min et al. (2021) in lettuce leaves and that of Marcelis (1993) in cucumber leaves and fruits. Therefore, even though the rate of dry weight growth at later stages was substantially higher in the treatment with gradually increasing PPFD compared to the treatment with a gradually declining PPFD, the fresh weight growth rate showed only a slight increase. Consequently, the final fresh weight was not significantly affected by the distribution of the light over the cultivation period.

4.3. Shelf life was not affected by increasing or decreasing light treatment

Min et al. (2021) observed that an increase in PPFD at the end of the production improved overall visual quality which correlated with an increase in carbohydrates and total ascorbic acid. However, no differences in overall visual quality and shelf life among treatments were found in the present study. During the last three days of our experiment PPFD ranged from 140 to 300 μmol m^{-2} s^{-1}. The strong effects on shelf life found by Min et al. (2021) occurred when differences in PPFD

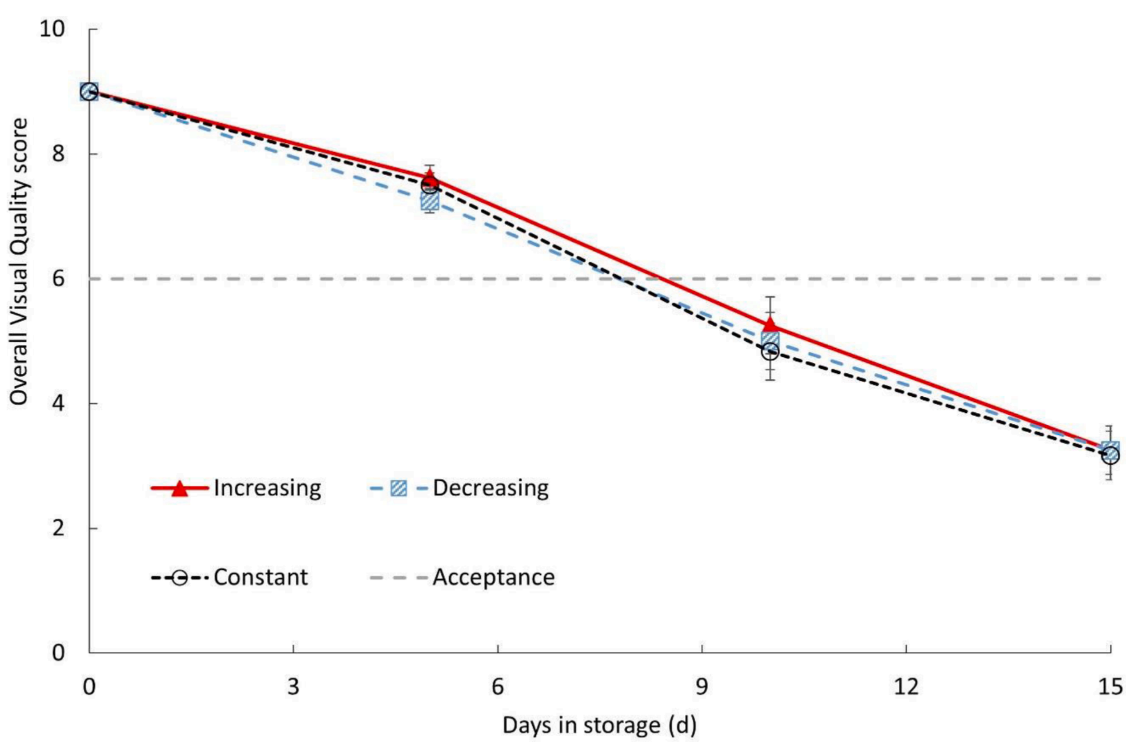

Fig. 8. Time course of overall visual quality scores in 12 °C storage. Error bars represent standard error of means. Treatment effects were not significant ($P = 0.05$). Data are the means of four repetitions ($n = 4$).

shortly before harvest were a bit larger than in the present study (210 versus 50 and 470 versus 210 μmol m^{-2} s^{-1}) during the last six days before harvest, while there was little difference in shelf life between treatments of 110 and 270 μmol m^{-2} s^{-1}). Hence, the absence of significant effects of the light treatments on shelf life in the present study is in line with the results of Min et al. (2021). The higher dry matter content found in the treatment where PPFD gradually increased is often assumed to be positive for a longer shelf life (reference) (Min et al., 2021).

The positive effects on dry matter content found in this study and the positive effects on shelf life, vitamin C, and carbohydrates found by Min et al. (2021) suggest that when stronger changes in PPFD would have been applied than in the present experiment more positive effects might have been found.

5. Conclusion

Gradually increasing PPFD during the cultivation of lettuce, while total light integral is kept constant, improves light use efficiency based on incident PPFD (dry weight production per unit of incident light) by 16 or 13% compared to treatments with decreasing or constant PPFD, respectively. However, the light use efficiency based on intercepted PPFD was highest when PPFD gradually decreased during cultivation. When changing PPFD during cultivation specific leaf area and dry matter content continuously acclimate to the prevailing PPFD. Despite the increase in final shoot dry weight by the treatment where PPFD gradually increased, final shoot fresh weight was not significantly affected. Our results show that gradually increasing PPFD had a positive effect on biomass accumulation, increased dry matter content but did not affect the shelf life.

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CRediT authorship contribution statement

Wenqing Jin: Conceptualization, Investigation, Formal analysis, Data curation, Writing – original draft. **Yongran Ji:** Investigation, Writing – review & editing. **Dorthe H. Larsen:** Investigation, Writing – review & editing. **Yang Huang:** Investigation, Writing – review & editing. **Ep Heuvelink:** Conceptualization, Formal analysis, Funding acquisition, Supervision, Writing – review & editing. **Leo F.M. Marcelis:** Conceptualization, Formal analysis, Funding acquisition, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability

Data will be made available on request.

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