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Partially Substituting Top-light with Intracanopy Light Increases Yield More at Higher LED Light Intensities

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Abstract. **This study compared supplemental white light-emitting diode (LED) light provided on top of the canopy (top-light) or partially on top and partially as intracanopy light (ICL) in high-wire cucumber (*Cucumis sativus*) and tomato (*Solanum lycopersicum*) crops. The aim was to determine the effects of partially substituting top-light by ICL on fruit yield and its underlying yield components. For each crop, three replicate Venlo glasshouse compartments were used. Two cucumber (HiPower and Skyson) and two tomato cultivars (Brioso and Merlice) were planted in the second half of Oct 2020 and grown on stone wool for a period of 15 weeks (cucumber) or 20 weeks (tomato). Light was supplied at either a light intensity of 250 or 375 μmol·m^{-2}·s^{-1}, provided either as 100% top-light or as 67% (2/3) top-light and 33% (1/3) ICL. For cucumber at the higher light intensity, 50% more fruits were retained and for tomato at the higher light intensity, planting density was 50% higher to keep the plants balanced in terms of source-to-sink ratio. Substituting 33% of top-light with ICL resulted on average in an increase of 17% in fresh fruit yield for both cucumber and tomato. This increase was twice as high at the higher light intensity (20% to 24%) compared with the lower light intensity (10% to 12%). For both cucumber and tomato, the higher yield for ICL treatments resulted mainly from higher total plant dry weight, whereas partitioning to the fruits was hardly affected. For both crops, the higher plant dry weight resulted from a higher light use efficiency. Increasing light intensity from 250 to 375 μmol·m^{-2}·s^{-1} resulted in 38% higher total daily light integral (including solar radiation) and 36% to 37% higher total plant dry weight in cucumber. In tomato, the higher light intensity resulted in 33% higher daily light integral and 36% to 40% total plant dry weight. These values are in agreement with the rule of thumb that 1% increment in light results in 1% increase in plant growth. For cucumber, partially substituting top-light by ICL as well as increasing light intensity resulted in longer and greener fruits, whereas tomato fruit quality (Brix, pH) was unaffected by ICL or light intensity. In conclusion, partially substituting top-light by intracanopy light increased fruit yield and this was even more so at higher than at lower supplemental light intensities.**

Yield and quality of vegetables and ornamentals produced in greenhouses can be improved using supplemental lighting (Stanghellini et al. 2019). In northern countries, such as the Netherlands, Norway, Sweden, Finland, and Canada, supplemental lighting is essential to allow for year-round production of vegetables like tomato and cucumbers (Moe et al. 2006). Tomatoes and cucumbers are among the most important horticultural crops that are often grown in greenhouses equipped with supplemental lighting in northern countries. Supplemental lighting is usually provided with high-pressure sodium lamps (HPS), but LEDs are taking over, because of a much higher efficacy (μmol light per J electricity) than HPS (Kusuma et al. 2020). In addition, LEDs operate at a much lower temperature than HPS lamps and therefore can be used in-between the canopy as intracanopy lighting (ICL) as well, to provide light to the lower leaves, which are more shaded compared with top leaves. Therefore, supplemental light is expected to be used more effectively by these lower leaves compared with top leaves that operate already closer to light saturation. Furthermore, supplying part of the supplemental light as ICL decreases the number of lamp fixtures above the crop, thereby decreasing the loss of solar light by shading. It also has the (theoretical) advantage of lowering the amount of light loss due to reflection by the canopy to the greenhouse cover.

Leaves lower in the canopy have a lower photosynthetic capacity due to acclimation to lower light levels (Trouwborst et al. 2011). Providing light to leaves lower in the canopy (ICL) did indeed increase leaf photosynthetic capacity (Dueck et al. 2012). By supplying light not only on top of the canopy, but also within the canopy, a more homogeneous vertical light distribution can be achieved. However, although vertical light distribution is improved by ICL, horizontal light distribution may be less uniform and more light that is not intercepted by leaves may reach the floor. Schipper et al. (2023) showed in a simulation study using a functional-structural plant model for a tomato crop, that combined ICL and top-lighting (50%/50%) had in all directions a more uniform light absorption than ICL or top-lighting alone.

Paponov et al. (2020) observed that tomato yield was increased by 21% when supplemental LED ICL (154 μmol·m^{-2}·s^{-1}; red-blue ratio 4:1) was applied compared with HPS top-lighting (420 μmol·m^{-2}·s^{-1}) alone. However, it should be noted that in their study, the total supplemental light intensity was higher when ICL was applied. Therefore, it is not clear whether the increase in yield is due to ICL, or (at least partly) due to the increased total light intensity. The difference in light spectrum (HPS for top-light, LED for ICL) may also play a role here. Pettersen et al. (2010) observed an increase of 12% in cucumber yield when 35% of the supplemental light was supplied as ICL (using HPS), compared with conditions in which 100% of the supplemental light was supplied as top-light, thereby keeping total light intensities of both treatments equal at 425 μmol·m^{-2}·s^{-1}.

Yield increase resulting from partially substituting top-light by ICL could result from more fruits harvested and/or a higher individual fruit weight. Jokinen et al. (2012) observed that the addition of ICL in sweet pepper resulted in an increase in the number of fruits and a decrease in the period from anthesis until fruit ripening. Paponov et al. (2020) found that supplemental ICL increased final weight of individual tomato fruits. However, by supplying ICL, also the total intensity of supplemental light was increased in the experiments of Jokinen et al. (2012) and Paponov et al. (2020). To analyze differences in yield and to determine which underlying components explain these differences, a yield component analysis is an excellent tool. Such an analysis has been conducted by Higashide and Heuvelink (2009) to explain why modern tomato cultivars obtain higher yields than older cultivars and by Ji et al. (2019) to analyze effects of far-red radiation on tomato yield. To the best of our knowledge, no detailed yield component analysis for partial substituting top-light by ICL has been published so far.

The aim of this study was to determine the effects of partially substituting top-light by ICL on fruit yield and which underlying yield components were responsible for the observed effects on yield in high-wire cucumber and tomato. We hypothesize that ICL increases fruit yield as a result of increased canopy photosynthesis, light use efficiency, and total dry matter production. This effect is expected to be larger at higher supplemental light intensity, as the leaves at the top of the canopy are already closer to light saturation.

Materials and Methods

Plant material and growing conditions. Tomato (*Solanum lycopersicum* 'Merlice', De Ruiter Seeds, The Netherlands and 'Brioso', Rijk Zwaan, The Netherlands) and cucumber (*Cucumis sativus* 'HiPower', BASF Vegetable Seeds, Nunhems, The Netherlands and 'Skyson', Rijk Zwaan, The Netherlands) plants were obtained from a young-plant propagator (Beekenkamp, The Netherlands). Tomatoes were sown on 12 Sep 2020 and transplanted on 29 Oct 2020, whereas cucumbers were sown on 28 Sep 2020 and transplanted on 21 Oct 2020. Tomato plants were grafted on rootstock 'Maxifort' (De Ruiter Seeds, The Netherlands) and topped above the third leaf, resulting in two stems per plant. Plants were transplanted in six (three replicate compartments for each crop) Venlo-type 144 m^2 glasshouse compartments of Wageningen University and Research (52°N, 5°E). Plants grown on stone wool cubes were placed on stone wool slabs of 1 × 0.2 × 0.1 m (l × w × h; Vital NG 2.0, Grodan, The Netherlands) which were placed on gutters. The top of the stone wool cubes was 0.4 m above the floor and the distance between two gutters was 1.5 m. Both crops were grown according to a high-wire V-system, for a period of 15 (cucumber) or 20 (tomato) weeks.

Day temperature was set to 22 to 23 °C, whereas night temperature was set to 19.5 °C for tomato and 21 °C for cucumber and adapted weekly based on plant status. Night was defined as the time between sunset and sunrise, regardless of the supplemental lights being turned on or off during this period. Initially only 5 h of supplemental light was applied, which increased over a period of 3 weeks to a maximum of 16 h in cucumber and over a period of 10 weeks to 14 h in tomato. For cucumber, the duration of supplemental lighting was decreased to 14 h after 9 weeks based on Vortus' advice. Supplemental lighting was turned off 30 min before sunset for both crops. During the light period, CO_2 concentration was kept at 600–700 ppm. Realized temperatures were similar for all compartments per crop (Supplemental Table 1). Relative humidity was kept at 70% to 80% in all compartments. Climate control inside the greenhouse compartments was conducted using a climate computer (Hoogendoorn, The Netherlands).

Light treatments. Each compartment was split into four equal-sized plots (6 × 4.5 m) using white plastic film and in each plot on two adjacent gutters one cultivar was grown, on the other two gutters the other cultivar was grown. Each plot in a compartment had one light treatment (allocated in a systematic way such that effect of light treatment would not get entangled with position in a compartment), consisting of either top-light only or top-light combined with ICL, and either a total light intensity of 250 or 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The ICL intensity was one-third of the total supplemental light intensity. Top-lighting consisted of nine broad-spectrum white LED modules (VYPR2P containing PhysioSpec R4 spectrum; Fluence, Austin, Texas, USA; Fig. 1), situated 3.85 m above the ground, evenly distributed in a 3 × 3 grid. In two of the four plots in each compartment, ICL broad-spectrum white LED modules (VYNE ICL prototype modules with PhysioSpec R3a spectrum; Fluence, Austin, Texas, USA; Fig. 1) were installed in three tiers above each gutter. Initially, ICL lights were situated at 1.40, 1.90, and 2.40 m above the floor in both crops. In tomato, the ICL modules were relocated to a height of 1.7, 2.0, and 2.4 m after 11 weeks of cultivation as removal of the lower leaves progressed.

The implemented light intensities were 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ top-light (TL250), 167 $\mu mol \cdot m^{-2} \cdot s^{-1}$ top-light combined with 83 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ICL (TL + ICL250), 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ top-light (TL375) and 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ top-light combined with 125 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ICL (TL+ICL375). These were realized based on measurements before the start of the experiment in one compartment for cucumber and tomato each; light intensities were adjusted by using dimmers (Hydro-X TrolMaster; Nanolux Technology Inc, Viterbo, Italy). The same dimmer settings were applied to the other compartments. Dimming percentages were also checked by comparing light module specifications with measured light intensities and these did match. For top-light, an average value of a checkerboard design consisting of 54 measuring points in a horizontal plane at 3.20 m above the ground was measured. For ICL, light intensity was measured at 15 cm from the modules, in a checkerboard design consisting of 81 measuring points in a vertical plane.

Calculated over the whole growing period, 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ supplemental lighting accounted for 76%, and 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ accounted for 83% of the daily light integral (15.9 and 21.9 $mol \cdot m^{-2} \cdot d^{-1}$, including both solar and supplemental light) for cucumber. For tomato, this was 66% and 74% for 250 and 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively, and the total light sum was 16.5 and 21.9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively. Total solar radiation was calculated from measured global radiation intensities ($W \cdot m^{-2}$) above the greenhouse, converted to $mol \cdot m^{-2}$ using a conversion factor of 4.6 mol per MJ photosynthetic active radiation (PAR) (Thimijan and Heins 1985), a greenhouse transmissivity of 0.62 (Li et al. 2015) and assuming that PAR is 50% of global radiation (energy units; Szeicz 1974).

Crop management. In tomato, one out of three young leaves, located just below a flowering truss, was removed weekly to stimulate generative growth. Old leaves were removed weekly from the bottom, in such a way that ∼18 leaves were kept on each stem for 'Brioso' and ∼21 leaves for 'Merlice'. In cucumber, fully grown leaves were removed weekly from the bottom, leaving ∼27 fully grown leaves on the stem for 'HiPower', and ∼24 for 'Skyson'. Side-shoots were removed weekly in an early stage. Trusses of 'Brioso' were pruned to eight fruits per truss and for

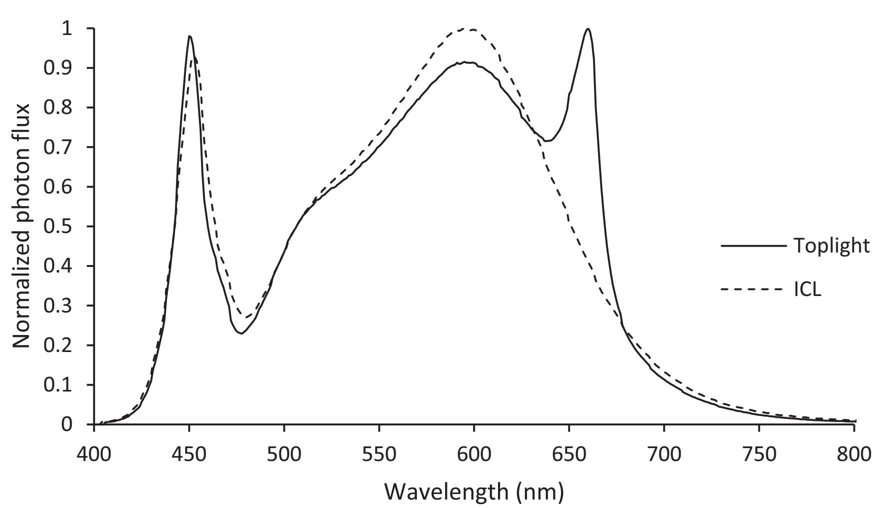

Fig. 1. Normalized photon flux density of the top (solid line) and intracanopy (dashed line) lighting. The fraction of photons emitted in the 400–499 nm, 500–599 nm, 600–699 nm, and 700–750 nm part of the spectrum was 14.7%, 40.9%, 42.2%, and 2.2% for top-light, and 16.0%, 44.3%, 37.0%, and 2.7% for ICL. Light spectrum was measured using the Apogee Field Spectroradiometer SS-110 (Apogee Instruments, Logan, UT, USA).

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'Merlice' this was five fruits per truss. Starting from January, the number of fruits per truss was increased to 10 for 'Brioso'. In cucumber, every other flower (50%; 1 in, 1 out) was removed from the stem at 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$, increasing this to two out of three (66%) from mid-December to early January. At 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ every third flower (33%; 2 in, 1 out) was removed. For cucumber, stem density was 2.74 m^2. For tomato, stem density was 2.74 stems per m^2 at 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 4.11 stems per m^2 at 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The reduced cucumber flower removal and increased tomato stem density at the high light intensity were applied to keep the plants balanced in terms of source-to-sink ratio.

Plants were drip-irrigated with a standard cucumber and tomato nutrient solution (Supplemental Table 2). Drip irrigation started 2 h after the supplemental lighting was turned on and irrigation frequency was adjusted during the cultivation period; irrigation stopped 2 h before the supplemental lighting was turned off. Electrical conductivity (EC) of the drip irrigation was 3.6 and 3.2 $dS \cdot m^{-1}$ for tomato and cucumber, respectively, EC in the stone wool slabs was ~4.7 and ~3.9 $dS \cdot m^{-1}$, respectively, for tomato and cucumber.

Measurements. Measurements were always conducted on the same six randomly selected stems on the gutter closest to the middle of each plot (excluding border plants) unless mentioned otherwise. The number of leaves larger than 2 cm was measured weekly until end of January and thereafter it was measured once in 3 weeks. Cucumber fruits were harvested when they reached ~300 g fresh weight, tomato trusses were harvested when all fruits on a truss had colored red. Fresh and dry weight of removed leaves and harvested fruits were determined. Also, the number of harvested trusses and fruits was counted. Fruit growth period was defined as the number of days between anthesis and harvest and was calculated for the median fruit (in cucumber) or truss number (in tomato) using linear regression on anthesis and harvest data.

After 15 weeks of cultivation for cucumber and 20 weeks of cultivation for tomato, plants were measured destructively. The total number of leaves larger than 2 cm still on the stem was counted and leaf area of these leaves was determined (LI-COR Leaf Area Meter, LI-3100). Dry weight (ventilated oven 8–24 h at 70 °C, followed by 36–72 h at 105 °C, depending on the plant part) of stems, leaves and unripe fruits that were still on the stems was also determined. Light use efficiency (LUE) was calculated as total dry matter production (g) divided by the total incident light integral (supplemental light plus solar light; mol) over the whole cultivation period.

For tomato fruits Brix value and pH were measured every 2 weeks on three harvested tomatoes per plot. Juice of the third tomato on the truss was used to determine Brix using a hand refractometer (Euromex, Arnhem, the Netherlands) and pH using a bench top HI2200 pH meter (calibrated at pH 4.0 and 7.0; Hanna Instruments, Leighton Buzzard, United Kingdom). Fruit length was determined for 17–25 cucumber fruits per plot, 14 weeks after transplanting. Chlorophyll content of the fruit peel was determined 13 weeks after transplanting. The peel of three representative fruits of each plot, was removed with a thin slicer. Of each fruit, three disks with a diameter of 5.5 mm, were taken out of the peel and placed in a glass vial, containing 4 mL of DMF (N,N-dimethylformamide), after which they were stored at −20 °C. After 2 weeks, the absorbance of the extract at 663.8 and 646.8 nm was measured using a Cary 4000 spectrophotometer (Varian Instruments, Walnut Creek, CA, USA), after which the chlorophyll content ($Chl_a + Chl_b$; $\mu g \cdot mL^{-1}$) was calculated based on the equations provided by Wellburn (1994):

$$Chl_a = 12 \cdot A_{663.8} - 3.11 \cdot A_{646.8}$$
$$Chl_b = 20.78 \cdot A_{646.8} - 4.88 \cdot A_{663.8}$$

Statistical analysis. For each crop, the four combinations of light intensity and light position were randomized over the four main plots in each compartment. Within each main plot, the two cultivars have been positioned. The values of six plants for the same treatment, cultivar, and compartment were averaged. All data were analyzed using GENSTAT (VSN International, Hemel Hempstead, United Kingdom). For each crop, a split-plot analysis of variance in three blocks was conducted, with the combination of light intensity (250 or 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and light position (top-light or partial ICL) as main factor, and cultivar as split-factor. With some exceptions, no significant interactions were observed between cultivar and light intensity nor between cultivar and light position, hence averages of both cultivars for each crop are shown. For reasons of clarity, averages over both cultivars have been presented also for the exceptional cases; however, observations per cultivar are provided in the supplementary material. For all variables, residuals could be assumed to be normally distributed according to the Shapiro-Wilk test for normality ($P = 0.05$). Equal variance was assumed and not tested due to a limited sample size (three repetitions of six plants each). Mean separation was conducted by Fisher's protected least significant difference test at $P = 0.05$.

Results

Yield. Averaged over both cultivars and light intensities, fruit fresh yield was higher for both cucumber (13% to 22%; Fig. 2; Supplemental Fig. 1 and Supplemental Table 3) and tomato (17% to 18% higher; Fig. 2; Supplemental Fig. 1 and Supplemental Table 4) when 33% of the supplemental top-light was substituted by intracanopy light. This increase was twice as high at the higher light intensity (20% to 24%) compared with the lower light intensity (10% to 12%; Fig. 2). Increasing the light intensity from 250 to 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased total fruit fresh yield by 64% to 73% averaged over both cucumber cultivars and 38% to 41% averaged over both tomato cultivars. It should be noted that for cucumber plants at the high light intensity fewer flowers were removed by pruning and for tomato, plants at the high light intensity were grown at a higher planting density.

Fruit dry weight showed the same trend as fruit fresh weight. Fruit dry weight was higher when 33% of the supplemental light was supplied by ICL in both cucumber and tomato (Fig. 2; Supplemental Fig. 1) cultivars. Increasing the light intensity from 250 to 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased fruit dry weight for both cucumber and tomato cultivars.

LUE (g plant dry weight per mol incident light) was higher, although not always statistically significant, when 33% of the supplemental light came from ICL, compared with 100% top-light in both cucumber and tomato (Fig. 2; Supplemental Fig. 2) cultivars. For both tomato and cucumber, this difference was larger at the higher light intensity.

The total number of harvested fruits was higher for the higher light intensity (Table 1; Supplemental Tables 5 and 6 for individual cultivars). It should be noted that at the higher light intensity in cucumber fewer flowers were removed by pruning while in tomato a higher planting density was applied. Number of fruits was not different between 33% ICL and 100% top-light. In tomato, neither light intensity nor light position affected the total number of harvested trusses. In cucumber, individual fruit weight was 11% higher when 33% of the top-light was substituted by ICL (Table 1). This difference was higher at the higher light intensity. In tomato, individual fruit weight was neither affected by light position nor light intensity (Table 1). Hence, in cucumber this increase in yield when 33% top-light was substituted by ICL mainly results from an increase in individual fruit weight, whereas the total number of fruits was unaffected by light position (Table 1). In tomato, the increase in yield resulting from partial substituting top-light by ICL resulted from small increases in both the number of fruits per plant and the individual fruit weight (although both not statistically significantly different; Table 1).

In both tomato and cucumber, the period that a fruit was growing on the plant was neither affected by light position nor light intensity. In tomato, fruit dry matter content was neither affected by light position, nor by light intensity for both cultivars. In cucumber, at the higher light intensity fruit dry matter content increased when 33% of top-light was substituted by ICL (Table 1).

Dry matter production and partitioning. Total plant dry weight at the end of the experiment was higher when 33% of the supplemental top-light was substituted by ICL in both cucumber and tomato (Table 1). For all four cultivars, this difference was larger at the higher light intensity (Supplemental Tables 7 and 8). ICL increased the total plant dry weight by 13% to 15% in cucumber (both cultivars) and 13% to 14% in tomato (both cultivars). For cucumber, higher light intensity and to a lesser extent application of ICL, resulted in slightly higher fraction of dry matter partitioned to the fruits, whereas less dry weight was partitioned to the leaves and stems (Supplemental Table 7). For both

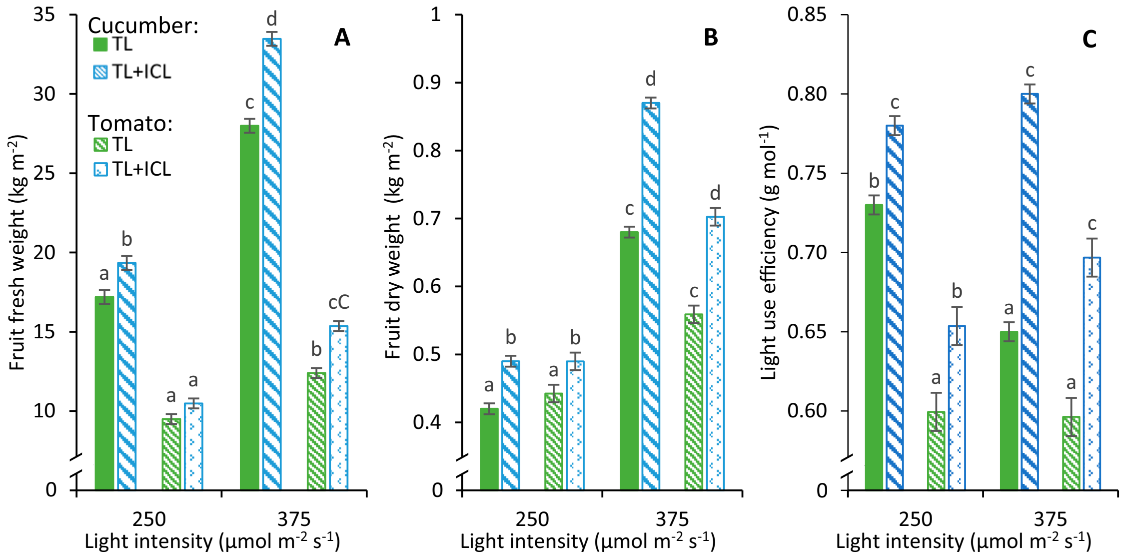

Fig. 2. Cucumber and tomato fruit fresh weight (yield; **A**), fruit dry weight (**B**) and light use efficiency (LUE; **C**), averaged over cucumber 'HiPower' and 'Skyson' after 15 weeks of cultivation, and tomato 'Brioso' and 'Merlice' after 20 weeks of cultivation. Supplemental light was supplied at 250 or 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$, as top-light (TL) or 33% of top-light substituted by intracanopy light (ICL). LUE is based on total plant dry weight and incident photosynthetically active radiation (PAR) (both supplemental light and solar radiation). Values are based on three replicates of six plants per cultivar. Error bars indicate the standard error of the treatment means, based on the common variance. Different letters indicate statistically significant differences according to Fisher's protected least significant difference test based on a two-way analysis of variance that was performed for each cultivar separately (Supplemental Tables 3 and 4).

tomato cultivars neither light intensity nor light position affected the partitioning of dry matter among the different plant organs (Supplemental Table 8).

Yield component analysis. For both cucumber and tomato, the higher fruit fresh yield when 33% of top-light was substituted by ICL resulted from a higher fruit dry weight, whereas fruit dry matter content slightly increased (Fig. 3). This higher fruit dry weight resulted from a higher total plant dry weight, whereas partitioning to the fruits was not much affected. A higher LUE when part of the supplemental light was provided by ICL caused this higher total plant dry weight.

Plant morphology. For cucumber, ICL did not affect stem length; however, stem length was 6% to 8% higher for plants grown at a total supplemental light intensity of 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared with 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Table 2; values per cultivar in Supplemental Table 9). For tomato, stem length was not influenced by light intensity or light position (Table 2; values per cultivar in Supplemental Table 10). For both tomato and cucumber, the number of leaves was unaffected by light intensity or light position. For cucumber, leaf area index (LAI) was unaffected by light intensity or light position Table 2). However, for tomato LAI was 28% to 42% higher when plants were grown

Table 1. Number of trusses and total number of harvested fruits, individual fruit weight, fruit growth period, and fruit dry matter content, averaged over cucumber 'HiPower' and 'Skyson' and tomato 'Brioso' and 'Merlice'. Cucumber was measured after a cultivation period of 15 weeks, whereas this was 20 weeks for tomato. Supplemental light was supplied at 250 or 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ as top-light (TL) or 33% of top-light substituted by intracanopy light (ICL). Number of trusses was only measured for tomato, indicated with a "-" for cucumber. Averages for total dry weight are based on three replicates of six plants per cultivar.

Treatment	Number of trusses/m^2	Number of fruits/m^2	Individual fruit wt (g/fruit)	Fruit growth period (d)	Fruit dry matter content (%)	Total dry wt (kg/m^2)
Cucumber:						
TL 250	-	77 a[i]	248 a	19.8 ab	2.51 ab	1.06 a
TL + ICL 250	-	80 a	259 b	18.4 a	2.56 b	1.13 b
TL 375	-	118 b	252 ab	20.5 b	2.49 a	1.36 c
TL + ICL 375	-	118 b	294 c	19.3 ab	2.63 c	1.64 d
SEmean[ii]	-	*1.862*	*2.924*	*0.417*	*0.017*	*0.017*
P value (intensity)[iii]	-	*<0.001*	*<0.001*	*0.099*	*0.220*	*<0.001*
P value (position)[iii]	-	*0.521*	*<0.001*	*0.020*	*0.001*	*<0.001*
P value (intensity × position)[iii]	-	*0.338*	*0.002*	*0.780*	*0.040*	*<0.001*
Tomato[iv]:						
TL 250	20 a[i]	199 a	63 a	62.0 a	4.87 a	1.38 a
TL + ICL 250	19 a	200 a	70 a	60.3 a	4.87 a	1.50 b
TL 375	19 a	264 b	61 a	63.7 a	4.69 a	1.82 c
TL + ICL 375	20 a	300 b	67 a	59.1 a	4.74 a	2.13 d
SEmean[ii]	*0.331*	*12.23*	*2.782*	*1.463*	*0.093*	*0.034*
P value (intensity)[iii]	*0.656*	*<0.001*	*0.453*	*0.868*	*0.143*	*<0.001*
P value (position)[iii]	*0.532*	*0.185*	*0.054*	*0.073*	*0.810*	*<0.001*
P value (intensity × position)[iii]	*0.339*	*0.216*	*0.980*	*0.370*	*0.784*	*0.036*

[i] Means followed by different letters differ significantly according to Fisher's protected least significant difference test at $P = 0.05$.
[ii] SEmean represents the standard error of the treatment means, based on the common variance.
[iii] *P* value represents the F-probability for treatment effect in a split-plot analysis of variance (light intensity, light position, and the interaction between intensity and position as main factors, cultivar as split-factor).
[iv] Means for each tomato cultivar separately are shown in Supplemental Tables 6 and 7. Number of trusses showed a significant interaction among light intensity, light distribution, and cultivar. Number of fruits showed a significant interaction between light intensity and cultivar. Individual fruit weight showed a significant interaction between light distribution and cultivar.

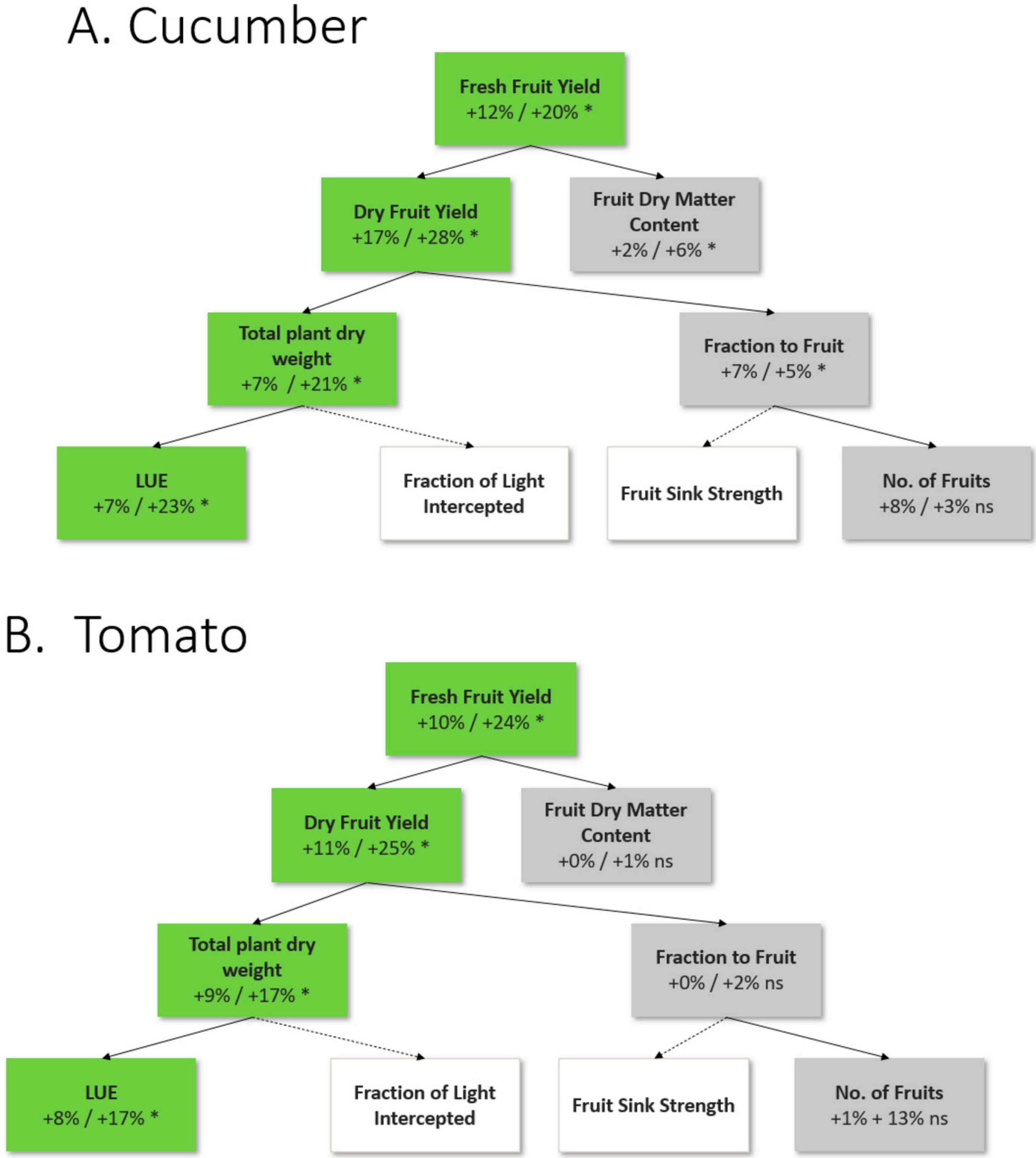

Fig. 3. Yield component analysis for cucumber (**A**) and tomato (**B**) averaged for both cultivars. Percentual increases when comparing 33% ICL with 100% top-light at 250 (left value) or 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (right value). Green boxes indicate significant ($P < 0.05$) increases (*), gray boxes indicate small to no differences, and white boxes indicate "not measured."

under a light intensity of 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared with 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$, a result of the higher planting density at higher light intensity (Table 2). A higher light intensity resulted in thicker leaves [lower specific leaf area (SLA)] for both cucumber and tomato (Table 2).

Fruit quality. Cucumber fruits were longer when 33% of the supplemental light was provided by ICL compared with 100% top-light (Table 3; Supplemental Table 11). Peel chlorophyll content was 16% to 23% higher when 33% of the top-light was substituted by ICL (Table 3; Supplemental Table 11). A higher light intensity also resulted in longer fruits with a higher peel chlorophyll content. Neither light intensity nor light position significantly affected tomato fruit Brix and pH values (Table 3; Supplemental Table 12).

Discussion

Partially substituting top-light with ICL increased fruit yield as a result of higher plant dry weight. Supplying 33% of the supplemental light by ICL resulted in a higher total plant dry weight in both cucumber and tomato, compared with 100% top-light (Table 1). This was caused by a higher LUE (Figs. 2

Table 2. Stem length, number of leaves per stem, leaf area index (LAI), and specific leaf area (SLA), averaged over cucumber 'HiPower' and 'Skyson' and tomato 'Brioso' and 'Merlice'. For cucumber, stem length, number of leaves, LAI, and SLA were determined 15 weeks after transplanting, whereas for tomato, this was 20 weeks. Plants grown at 250 or 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ supplemental light applied as top-light (TL) or 33% of top-light substituted by intracanopy light (ICL). Averages are based on three replicates of six plants per cultivar.

Treatment	Stem length (m)	Number of leaves	LAI ($m^2 \cdot m^{-2}$)	SLA ($m^2 \cdot kg^{-1}$)
Cucumber:				
TL 250	9.8 b[i]	103 a	3.65 a	38.0 b
TL + ICL 250	9.8 b	104 a	3.32 a	39.3 b
TL 375	9.1 a	105 a	3.56 a	34.3 a
TL + ICL 375	9.2 a	102 a	3.37 a	33.2 a
SEmean[ii]	*0.165*	*1.236*	*0.161*	*0.540*
P value (intensity)[iii]	*0.007*	*0.841*	*0.896*	*<0.001*
P value (position)[iii]	*0.615*	*0.306*	*0.152*	*0.900*
P value (intensity × position)[iii]	*0.896*	*0.242*	*0.670*	*0.071*
Tomato:				
TL 250	5.3 a[i]	69 a	4.17 a	25.2 bc
TL + ICL 250	5.3 a	68 a	4.10 a	25.3 c
TL 375	5.4 a	69 a	5.62 b	24.8 b
TL + ICL 375	5.3 a	69 a	5.56 b	24.1 a
SEmean[ii]	*0.109*	*1.172*	*0.130*	*0.131*
P value (intensity)[iii]	*0.793*	*0.793*	*<0.001*	*<0.001*
P value (position)[iii]	*0.894*	*0.902*	*0.626*	*0.056*
P value (intensity × position)[iii]	*0.650*	*0.568*	*0.966*	*0.037*

[i] Means followed by different letters differ significantly according to Fisher's protected least significant difference test at $P = 0.05$.

[ii] SEmean represents the standard error of the treatment means, based on the common variance.

[iii] *P* value represents the F-probability for treatment effect in a split-plot analysis of variance (light intensity, light position, and the interaction between intensity and position as main factors, cultivar as split-factor).

and 3) suggesting an increased canopy photosynthesis rate when part of the light is supplied by ICL. Leaves in the upper part of the canopy are often already near light saturated, whereas leaves lower in the canopy operate under light-limited conditions (Dueck et al. 2012). Pettersen et al. (2010) observed that the net photosynthetic rates of leaves at the bottom of the canopy increased by 70% in cucumber when 65% top-light and 35% ICL (using HPS lamps of 250 W) was supplied, compared with 100% top-light. These results conflict with Verheul et al. (2022), who observed a higher LUE for tomato grown at 100% HPS top-light compared with partial replacing HPS top-light with LED (red:blue 4:1) ICL. Plants receiving a daily light integral (DLI) of 30 $mol \cdot d^{-1}$ through HPS top-light had 42% higher yield compared with plants receiving the same DLI with a combination of HPS top-light and LED ICL.

Furthermore, where 100% top-light mainly irradiates the adaxial side of the top leaves, ICL also provides light to the abaxial side of the leaves, which results in a more uniform intraleaf light profile and thus potentially higher leaf photosynthetic rates as quantified by Terashima et al. (2009).

It should be noted that LED and HPS differ in spectrum, whereas in our experiment both top-light and ICL LEDs providing a white spectrum were used. Based on measured effects of spectrum of the top-light (Kusuma et al. 2022), we do not expect that in our experiment the observed positive effects of ICL are due to the small difference in spectrum between ICL and top-light (Fig. 1).

Observed tomato LUE values (Fig. 2) of ~0.65 $g \cdot mol^{-1}$ [with fraction fruit 0.5 and 5% fruit dry matter content this means 6.5 g fresh weight (FW)/mol] were at the lower end of the range (6.4 to 10.3 g FW/mol) reported by Verheul et al. (2022). However, 0.65 $g \cdot mol^{-1}$ is similar to 3 g per MJ PAR (3/4.6 = 0.65 $g \cdot mol^{-1}$) reported by Higashide and Heuvelink (2009).

Especially in tomato, partial replacing top-light by ICL did not affect partitioning to the fruits (Fig. 3). This is in agreement with Heuvelink (1995), because trusses were pruned to a fixed number for fruits, hence higher assimilation availability in the ICL treatments could not affect partitioning indirectly by improved fruit set (Bertin 1995).

Partially substituting top-light with ICL is most effective at high supplemental light intensities. Averaged over both light intensities and all for cultivars, substituting 33% of top-light with ICL resulted in an increase of 17% in both cucumber and tomato yield, compared with supplying 100% top-light (Figs. 2 and 3). The effects of ICL were twice as high (20% to 24% yield increase) when a total light intensity of 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was applied compared with 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (10% to 12% yield increase; Fig. 3). A similar increase in yield as a result of the application of both top-light and ICL was observed by Paponov et al. (2020). These authors reported that the application of red-blue (ratio 4:1) intercrop lighting in tomato increased tomato fruit yield by 21% compared with when only top-light was supplied. However, it should be noted that in their study, ICL was added to top-light, resulting in a higher total supplemental light intensity when ICL was supplied. Similarly, also Verheul et al. (2022) reported a tomato yield increase when LED ICL was added to HPS top-light. However, this positive effect of supplemental LED ICL on yield decreased at higher amounts of HPS top-light. In the study of Hovi-Pekkanen and Tahvonen (2008), where the total light intensity of supplemental lighting was kept equal between the different light treatments, yield increased by 10% in a cucumber crop when 24% and 48% of the supplemental light was provided by ICL, compared with 100% top-light.

The positive results of ICL at high light intensity (375 $\mu mol \cdot m^{-2} \cdot s^{-1}$) could be partly due to the large fraction of green light in the ICL spectrum. Green light is able to penetrate deeper into the mesophyll layer of a leaf, but also through the whole canopy, resulting in a more uniform light distribution and potentially higher photosynthesis rates (Terashima et al. 2009).

Table 3. Cucumber fruit length and peel chlorophyll content averaged over 'HiPower' and 'Skyson' and tomato fruit pH and Brix averaged over 'Brioso' and 'Merlice'. Plants grown at 250 or 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ supplemental light applied as top-light (TL) or 33% of top-light substituted by intracanopy light (ICL). Averages are based on three replicates of three fruits (fruit peel chlorophyll content) or 17 to 25 fruits (fruit length). Tomato fruits were harvested over a period of 9 weeks and Brix and pH values are averages of 55 and 37 fruits, respectively, for each cultivar and light treatment.

	Cucumber		Tomato	
Treatment	Fruit length (cm)	Chlorophyll content ($\mu g \cdot mL^{-1}$)	Brix	pH
TL 250	24.1 a[i]	8.6 a	4.0 a[i]	4.1 a
TL + ICL 250	24.8 a	10.6 b	4.2 a	4.1 a
TL 375	25.6 b	10.6 b	4.0 a	4.1 a
TL + ICL 375	27.1 c	12.3 c	4.1 a	4.1 a
SEmean[ii]	*0.233*	*0.224*	0.064	0.026
P value (intensity)[iii]	*<0.001*	*<0.001*	0.271	0.415
P value (position)[iii]	*0.003*	*<0.001*	0.086	0.840
P value (intensity × position)[iii]	*0.139*	*0.745*	0.539	0.391

[i] Means followed by different letters differ significantly according to Fisher's protected least significant difference test at $P = 0.05$. Data for each cultivar separately are presented in Supplemental Tables 11 and 12.

[ii] SEmean represents the standard error of the treatment means, based on the common variance.

[iii] *P* value represents the F-probability for treatment effect in a split-plot analysis of variance (light intensity, light position, and the interaction between intensity and position as main factors, cultivar as split-factor).

Partial substituting top-light with ICL improves cucumber fruit quality. Fruit length and color of the fruit (quantified by peel chlorophyll content; Schouten et al. 2002) are important quality aspects of a cucumber fruit (USDA 2016). Both fruit length and total chlorophyll content were higher when 33% of the supplemental light was supplied by ICL (Table 3). This was also found by Hovi-Pekkanen and Tahvonen (2008). Supplying a higher light intensity increased cucumber fruit length and total chlorophyll content (Table 3). Lin and Jolliffe (1996) also reported improved external fruit quality indicated by greener fruits at higher light intensities, during an experiment performed in summer, where part of the fruits were shaded. These authors observed a positive relationship between the greenness of the fruit and postharvest shelf life. This suggests that partial substituting top-light by ICL may result in cucumbers with a prolonged shelf life.

Higher supplemental light intensity substantially improved growth and yield. Supplying a total supplemental light intensity of 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased yield by 68% in cucumber and 39% in tomato (averaged for both light positions and both cultivars; Fig. 2). The increase in yield resulting from the application of ICL was more significant under high light intensities in both crops. This can be explained by the fact that leaves in the top of the canopy grown under a supplemental light intensity of 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on top of the crop are operating closer to light saturation compared with leaves grown at 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Therefore, a reduction in light intensity would only slightly decrease leaf photosynthetic rates in the top leaves. However, it should be noted that by increasing the light intensity, also stem density was increased in tomato to keep the plants balanced in terms of source-to-sink ratio.

Supplemental light intensity of 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared with 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased total DLI (including solar radiation) by 38% and 33% in cucumber and tomato, respectively. This increase in light resulted in an increase in total plant dry weight by 36% to 37% in cucumber and 36% to 40% in tomato (Table 1). This agrees with the rule of thumb that suggests that an increase of 1% in light results in 1% more plant growth (Marcelis et al. 2006). Verheul et al. (2022) similarly observed that 1% increase in DLI resulted in 1% to 1.1% increase in tomato fruit yield, when comparing three HPS top-light intensities.

Higher light intensities did not result in a higher number of leaves in both crops, nor did it affect the LAI in cucumber. In tomato, LAI was higher when a total supplemental light intensity of 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was applied compared with 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$. However, at the higher light intensity, a higher planting density was applied, resulting in this higher LAI. SLA was lower at higher light intensity (Table 2), indicating thicker leaves. This agrees with the results of Fan et al. (2013), who observed a lower SLA at higher light intensities in young tomato plants. In addition, the meta-analysis of Poorter et al. (2009), summarizing a large number of experiments with different plant species, shows a nonlinear increase in leaf dry mass per unit area (LMA, inverse of SLA) with DLI.

For cucumber, a total supplemental light intensity of 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ resulted in a higher fraction of the total dry weight partitioned to the fruits compared with a total supplemental light intensity of 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Supplemental Table 7). This is most likely the result of the flower removal strategy, where more fruits were retained on the plants at the higher light intensity and therefore a higher fraction of dry matter was partitioned to the fruits (Marcelis 1993). This may also explain why 1% more light resulted in 1% more cucumber plant growth; however, in 2% more fruit fresh yield. In tomato, dry matter partitioning did not differ between the two light intensities (Supplemental Table 8). This is in agreement with Heuvelink (1995) who reported that higher assimilate availability did not affect partitioning in tomato as long as an indirect effect of improved fruit set was excluded.

Substituting part of top-light by ICL clearly has a positive effect on yield in both tomato and cucumber, and this increase is higher at higher supplemental light intensity. For greenhouse growers, this would lead to a decision in favor of ICL, as higher yield usually results in a higher revenue. However, to make a positive business case for the use of ICL, also financial aspects like investment costs, labor costs for cleaning and maintaining the fixtures, as well as practical complications for crop management and starting and ending cultivation cycles need to be taken into account. Consequently, tomato or cucumber growers might still be in favor of using only top-light, despite the higher yield for ICL.

In the present study, one-third of the top-light was replaced by ICL. Further research should reveal whether a different, most likely higher fraction will improve yield even further. Furthermore, the spectrum of top-light and ICL were the same. Further research should reveal whether specific ICL spectra may improve yield even further. To the best of our knowledge, no specific studies on the role of ICL spectra have been conducted. Because far-red radiation has been shown to increase yield in tomato (Ji et al. 2019), this may deserve specific attention, as in the present experiment only a very small part (Fig. 1; 2.7%) of the photons were in the far-red region. Furthermore, in our study both top-light and ICL contain a large fraction of green light. Green light is known to be transmitted by leaves more than red or blue (Terashima et al. 2009). In this respect, it would be interesting to examine the effect of partially replacing top-light by ICL with red/blue LEDs.

Conclusion

Supplying 33% of the supplemental light by ICL resulted in 17% increase in cucumber and tomato fruit yield, compared with 100% top-light (averaged over both cultivars and both light intensities). This increase was twice as high at the higher light intensity (20% to 24%) than at the lower light intensity (10% to 12%). In both cucumber and tomato, this increase in yield was mainly the result of a higher total plant dry weight.

At 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared with 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$, fruit yield was 68% higher for cucumber and 39% for tomato. This was mainly the result of higher total plant biomass and in cucumber also a higher fraction of dry weight partitioned to the fruits. Moreover, 1% more light resulted in 1% more biomass in both crops, 1% higher fruit yield in tomato and 2% higher fruit yield in cucumber. It should be noted that at high light intensity, tomato plants were grown at a higher stem density, and for cucumber plants fewer flowers were removed by pruning to keep the source and sink of the plants balanced.

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