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Artificial top-light is more efficient for tomato production than inter-light.

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ABSTRACT

Studies of whole-plant responses of tomato to light environments are limited and cannot be extrapolated from observations of seedlings or short-term crops in growth chambers. Effects of artificial light sources like high pressure sodium (HPS) and light emitting diodes (LED) are mainly studied as supplement to sunlight in greenhouses. Since natural sunlight is almost neglectable in Norway during wintertime, we could study effects of different types of artificial light on crop growth and production in tomato. The goal of this experiment was to quantify the effects of artificial HPS top-light, installed at the top of the canopy, and LED inter-light, installed between plant rows, on fresh and dry matter production and fruit quality of greenhouse tomatoes under controlled and documented conditions. Our aim was to optimize yield under different light conditions, while avoiding an unfavourable source-sink balance. Tomato plants were grown under HPS top light with an installed capacity of 161, 242 and 272 W m^{-2} combined with LED inter-light with an installed capacity of 0, 60 or 120 W m^{-2}. We used stem diameter as a trait to regulate air temperature in different light treatments in order to retain plant vigour. Results show that both HPS top light and LED inter-light increased tomato yield. However, the positive effect of supplemental LED inter-light decreased at higher amounts of HPS top light. Under the conditions in this experiment, with neglectable incoming solar radiation, an installed amount of 242 Watt m-2 HPS top light and a daily light integral (DLI) of 30 mol m-2 day-1 resulted in best light use efficiency (in gram fresh tomato per mol). Addition of LED inter-light to HPS top light reduced light use efficiency. Results show that winter production using artificial light in Norway is more energy efficient compared to production under sunlight in southern countries. Results can be used for modelling purposes.

Keywords: High pressure sodium light, light emitting diodes, greenhouse production, fruit quality, light use efficiency, energy use efficiency, (Norway).

INTRODUCTION

The availability of natural light is the main limiting factor for plant production at northern latitudes, where supplementary light is necessary to assure year-round production. Addition of artificial light increases the daily light integral (DLI, the number of photosynthetically active photons that are delivered to a specific area over a 24-hour period) and improves both yield and product quality in greenhouse vegetables production (Dorais, 2003, Verheul et al., 2012, Heuvelink, 2018). High pressure sodium (HPS) lamps, mounted 1.5 m above the canopy, are used to both increase light intensity and temperature in northern greenhouses during wintertime. The efficiency of modern HPS lamps reaches 1.7-2.1 µmol photosynthetic active radiation (PAR) per joule of electricity (Gislerød et al., 2012). The development of high-power LEDs makes it possible to use LEDs for lighting in greenhouses as an alternative or a supplement to HPS lamps. LED lamps can be more efficient to convert electricity into light, varying between 1.4 and 3.6 µmol PAR J^{-1} electricity (DLC, The DesignLights Consortium, 2021), and have a much longer life span, of more than 50.000 h, compared to HPS lamps. Nowadays, LED systems usually consist of red LEDs, which are the most energy efficient, and a small fraction of blue LEDs. An advantage of LED systems is their low radiative heat emission, that allows to place the fixtures closer to the plants. For this reason, LED systems are often placed between plant rows in vertically trained, hedge grown crops like tomato and cucumber. Placement in a lower part of the canopy diminishes the strong light gradient from top to bottom. Intra-canopy LED lighting increases yield by an increase in the total assimilates available for fruit growth, stimulates photosynthetic rates in the lower-canopy leaves and prevents their premature senescence (Pettersen et al, 2010; Trouwborst et al., 2011; Dueck et al, 2012; Gomez and Mitchell, 2016, Paponov et al, 2018) and enhances root activity through an increase in root pressure and water supply to support fruit growth during the night (Paponov et al., 2020). The major disadvantages of LED systems are their investments costs, which make their economic viability questionable (Nelson and Bugbee, 2014; Persoon and Hogewoning, 2014). However, prices of LED systems are decreasing, and their electric efficiency is increasing.

Light can be measured in several unit systems (Thimijan and Heins, 1983), photometric units, radiometric units and photon or mol units. Photon or mol units are relevant for photosynthesis and crop growth. The number of photons received by the crop and individual leaves, expressed as photosynthetic photon flux density (PPFD) in µmol $m^{-2}s^{-1}$, is directly related to the photosynthesis rate or net CO_2 uptake rate, also expressed in µmol $m^{-2}s^{-1}$. Usually, only wavelengths between 400 and 700 nm are counted to contribute to leaf photosynthesis (McCree, 1972). LED systems with red (630-680 nm) and blue (440-460 nm) lights are within this spectrum. More recent investigations have shown that also far-red light (700-750 nm) can contribute to crop photosynthesis (Zhen and Bugbee, 2020). While red light is utilized most efficiently for photosynthesis, adding some (6–12%) blue light is advantageous for growth and yield in tomato production (Hogewoning et al, 2010; Davis and Burns, 2016; Kaiser et al., 2019). From an energetic point of view, radiometric measurements of light expressed in W m^{-2} are more relevant. The electric energy consumption of lamps per unit of cultivation area in W m^{-2} and the subsequent production volume of plants is directly related to the grower’s economy and to the development of energy efficient and sustainable production systems.

The intensity and uniformity of light received by individual leaves in a crop have a large effect on yield (Bugbee, 2016). The distribution of light from artificial light sources in an empty greenhouse is dependent on the placement of the lamps and the properties of their fittings and reflectors and can be measured precisely. In a crop however, due to the changing nature of plants and environment during the day and the growing season, it is more difficult to measure or calculate intensity and distribution of light on individual leaves at all time (Sarlikioti et al., 2011; De Visser et al., 2014; Dieleman et al., 2019). In addition will different wavelengths penetrate differently in the canopy and as such influence light distribution (Sun et al., 1998, Kaiser et al., 2019). Different placements of HPS and LED lamps lead to different light distribution patterns and thus to different effects on photosynthesis and yield.

Ultimately, the total light efficiency of different lamp types can be quantified by their effect on yield and biomass production of a defined crop under defined growth conditions. Plant responses to light sources or different light spectra have been examined largely for seedlings or short-term crops using sole-source or supplemental lighting. Studies of whole-plant responses to light environment are extremely limited and cannot be extrapolated from short-term observations of seedlings or short-term crops (Kim et al, 2019). Light efficiency of LED systems without the impact of solar radiation has been quantified in indoor multilayer growing systems (Kozai, 2018). However, HPS lamps are not suitable for such indoor multilayer systems, as the heat and thermal radiation they produce require a distance of at least 1.2 m from the crop. Light efficiency of HPS lamps, with and without addition of LED inter-light, have been studied in greenhouses (Dueck et al., 2012, Gajc-Wolska et al, 2013, Gomez and Mitchell, 2016; Moerkens et al, 2016; Yan et al., 2018). In almost all cases, HPS and LED were used as light supplementary to the natural sunlight, representing only a small contribution of the total amount of light. Little is known about effects of HPS lamps as single light source on producing plants. This makes it difficult to quantify effects of solely artificial light on growth and production.

The tomato crop growth, development and yield have been studied intensively, as well as effects of light, temperature, CO_2 concentration and relative humidity (Heuvelink, 2018). Quantifying effects of changing a single factor like supplemental light on growth and production is however complicated. The change of the level of one factor affects the optimum of other factors, which requires adjustment of these other factors to achieve full yield potential. Yield in crops like tomato and cucumber is not only determined by biomass production, but also by assimilate distribution to the fruits, leaves, stem and roots (de Koning, 1994). Adding supplemental light with no further adjustments in the climate setpoints and crop management may result in improved vegetative growth but little or no yield improvement. The adjustments in temperature, plant density and other factors needed to optimally transfer supplemental light into production are still not fully understood (Heuvelink et al., 2006). Models can help to understand plant reactions to climatic factors (Körner et al., 2009), but these models must be verified by experiments under strictly controlled conditions.

Optimal tomato production in greenhouses and good greenhouse management requires a balance between light and temperature resulting in a balance between source and sink, i.e. assimilates and growing organs (Stanghellini et al. 2019). In producing tomato plants, usually the sink is much bigger than the source (Li et al., 2015). The optimum temperature increases with increased light intensity. Under high light intensities and suboptimal temperature, the source can be bigger than the sink and plants develop thick and short stems and leaves. The produced assimilates are not distributed to the growing organs, like young leaves, roots, flowers and fruits, but stay in the assimilating and closely located organs, like leaves and stems (Stanghellini et al., 2019). Reduced carbohydrate partitioning to the fruits will reduce harvest index and yield. Higher temperature under high light intensity results in a better balance between source and sink. In addition, CO_2 assimilation might be increased since the photosynthetic apparatus of tomato plants is less stressed when high light intensity and high temperature is applied simultaneously instead of separately (Gerganova et al., 2016).

In greenhouse tomato crops, growers examine the ‘vigour’ of the tomato plants to choose cultivation techniques and optimize production. Stem diameter was defined to be an objective criterium for ‘vigour’ (Navarrete et al., 1997). Weekly increase in plant length, leaf length of the last fully developed leaf and the number of leaves on the plant are used to describe the vegetative state of tomato plants, whereas flowering rate, truss development rate and number of trusses on the plant describe the generative state of the plant (de Koning, 1994). In practical experiments and registrations in Norway for several growers and over several years, it was confirmed that a stem diameter of between 10 and 12 mm, measured at plant height one week before, about 20 cm below shoot apex, resulted a good balance between source and sink and highest tomato yields (Henk Maessen, personal communication).

It is expected that HPS top light and LED inter light will influence tomato taste properties (Dzakovich et al., 2015). Consumers appreciation and willingness to pay is influenced by the content of soluble solids, sugars and organic acids, contributing to the overall aroma intensity as well as firmness (Verheul et al., 2015). Tomato quality of off-season tomatoes has a negative reputation (Stevens et al.,1977; Kader et al., 1978; Watada and Aulenbach, 1979) and thus a lower value. It is observed that soluble sugar concentration of tomato fruit follows the pattern of solar radiation (Slimestad and Verheul, 2005). Quantification of the effects of light and light sources on production and production value should therefore include quantification of taste parameters.

During wintertime in Norway, the amount of natural sunlight is almost neglectable, and tomato production in greenhouses is only possible using relatively high amounts of artificial light (> 200 W m^{-2} of installed light). This gives us a unique possibility to study effects of different types of artificial light with little influence of solar radiation on crop growth and production on fully grown and producing tomato plants.

The goal of this experiment is to quantify effects of artificial HPS top-light and LED inter-light on fresh and dry matter production and fruit quality of greenhouse tomatoes under otherwise controlled and documented conditions. Our aim was to optimize yield under different light conditions, while avoiding an unfavourable source-sink balance. We used stem diameter as a trait to regulate air temperature in different light treatments.

These results can finally be used to calibrate, adjust and verify plant production and greenhouse climate models on effects of artificial light. Knowledge of the crop response can be used to manage greenhouse technology in the most economical way (Stanghellini et al., 2019).

MATERIALS AND METHODS:

The experiment was conducted in three identical and adjacent greenhouse compartments of each 224 m^2 (17.5 m x 12.8 m) with a gutter height of 6.0 m in the new greenhouse research facilities at NIBIO Særheim, located in southwestern Norway (58°47’N, 5°41’E). The greenhouse climate was regulated by a standard horticultural computer (Priva Connext), and climate conditions were measured every 5 minutes.

Plant materials and light treatments:

Tomato plants (*Lycopersicon esculentum* Mill.) variety ‘Dometica’ were raised in 0.5 L rockwool cubes and planted with a plant density of 3.0 plants per m-2 on the 17th of September 2018, at the time that the 2nd truss reached anthesis. Plants were planted on standard rockwool slabs (90 cm x 10 cm x 15 cm) placed on gutters at 80 cm height from the ground floor. On each rockwool slab, six plants were planted and trained as a high wire culture in a V-row system (Peet and Welles, 2005). The distance between rows was 90 cm and the distance between gutters was 180 cm.

Plants were subjected to three levels of high pressure sodium (HPS) lamps (Philips GP Plus 600 and 750 W, Gavita Nordic AS, Norway), mounted at a height of 6 meter, 1.5 meter above the top of the canopy, and three levels of LED lamps (Union Power Star 160 W, Munich, Germany) with 450 and 660 nm wavelength bands at a diode energy ratio of 20/80. The spectral distribution of HPS and LED lamps used in the experiment was measured with a spectrometer (JAZ COMBO, Ocean Optics Inc, USA) and shown in figure 1. LED lamps were installed emitting light horizontally in two directions in the middle of the V-row system at two heights (65 and 130 cm from the rockwool block) (as shown in Paponov et al., 2020) or four heights (65, 110, 150 and 195 cm from the rockwool block). Using this set-up, 97% of the light from HPS and LED lamps is intercepted by the plants (Paponov et al, 2020). Light treatments are summarized in table 1. The electric energy consumption of installed lamps per unit of cultivation area in W m^{-2}, or energy use of lamps, is described as the amount of light installed in W m^{-2}.

In an establishing phase of four weeks after planting, plants were grown under sunlight and a maximum of 12 hours of HPS lamps. HPS lamps were switched off automatically when the incoming natural light intensity from outside the greenhouse was more than 300 W m^{-2}. At the time that the top of the plant reached the hight of 150 cm from the rockwool cube, part of the plants were also submitted to LED lamps at two heights (65 and 130 cm from the rockwool block) switched on during 18h per day (04:00-22:00). The daylength of HPS lamps was increased to maximum 14h. At the time that the top of the plant reached a height of 190 cm from the rockwool cube, part of the plants were submitted to additional two LED lamps now divided over four heights within the canopy (65, 110, 150 and 195 cm from the rockwool block). The daylength of HPS lamps was increased to 18h (06:00-24:00). At this time of year, the incoming natural light intensity was less than 300 W m^{-2}.

Global radiation was measured with a Kipp solarimeter. The daily light integral (DLI, mol m−2 d−1) for global radiation was estimated based a light efficacy of 2.2 µmol J^{-1} and a light transmission factor of 0.65 from outside radiation to the top leaves of the crop due to the greenhouse cover and installed lamps.

Regulation of climatic conditions and irrigation:

Increased light intensity increases the optimal temperature for plant growth (Verheul et al, 2020). In order to secure optimum temperature for the different light treatments, plant vigour was measured once a week on two replications of each six plants for each treatment. Temperature set points, including two temperature levels during the day, a night drop after switching of the light for about two hours and another temperature during the rest of the night, were adjusted each week for each compartment based on plant vigour measurements. In order to keep a good vigour in each compartment, the temperature was adjusted to keep the thickness of the stem, measured at the height of plants one week before, in all treatments between 10 and 12 mm (Navarette et al., 1997). Greenhouse compartments were heated using conventional heating pipes. Ventilation tubes were placed beneath the plants to ensure optimal stirring of the greenhouse air.

Windows were opened and closed to regulate temperature and relative humidity. Windows were opened at 1 ^{o}C above the temperature set point. Pure CO_2 was supplied with a maximum capacity of 125 kg ha^{-1} h^{-1} during daytime in all three compartments. Pure CO_2 was provided with a set point of 1000 ppm when the windows were closed. CO_2 set point was reduced linearly depended on window opening to 600 ppm at maximum ventilation. CO_2 of greenhouse air was measured at 5 minutes interval with a gas analyser (Priva CO_2 monitor Guardian +). Air temperature and relative humidity were measured by dry- and wet-bulb thermocouples placed in ventilated boxes that shielded against direct solar radiation and placed in the middle of the canopy at a height of 1.5 meter. Thermocouples were calibrated before the start and controlled at the end of the experiment. Temperature (°C), relative humidity (%), CO_2 concentration (ppm) and window opening (%) were registered every 5 minutes. Heat energy consumption in each of the three greenhouse compartments was measured with energy flow meters (Sontex Superstatic 789, Sontex Switzerland).

Plants were drip irrigated with a complete nutrient solution based on standardized recommendations (de Kreij et al., 1999) containing the following: 26.43 mM NO3, 1.68 mM NH4, 2.23 mM P, 8.72 mM K, 10.63 mM Ca, 2.71 mM Mg, 2.67 mM S, 0.3 mM Na, 0.1 mM Cl and micronutrients with the following concentrations: 63 µmol Fe, 27 µmol Mn, 10 µmol Zn, 68 µmol B, 6 µmol Cu and 1.6 µmol Mo. The electrical conductivity of the nutrient solution was 3.6 mS cm^{-1}, the pH was 5.9, and the daily drainage percentage was 30%. Irrigation and drainage were registered continuously using a weighing scale (Priva GroScale) combined with a drainage sensor.

<u>Plant care and plant vigour measurement:</u>

Tomato flowers were pollinated by bumblebees. Pollination was checked daily. Plants were lowered weekly by about 30 cm, side shoots were removed, and three mature leaves were removed below the truss with fruits reaching turning stage (Gierson and Kader, 1986). The trusses were pruned to seven fruits per truss just after the fruit set of each truss. No pests or diseases were observed.

Plant vigour (stem diameter, increase in plant length, leaf length of the last fully developed leave, number of leaves on the plant) and fruit development (flowering rate, truss development rate, number of trusses and fruits on the plant) was measured once a week on two replications of each six plants per treatment. Stem diameter was measured at plant height one week before, about 20 cm below shoot apex.

Dry matter accumulation was assessed based on weekly measurements of plant length, number of leaves and number of fruits. The number of harvested leaves ware registered. Three times during the experiment, on 05.11.18, 26.11.19 and 17.12.19, ripened fruits and leaves were harvested for determination of fresh and dry weight (dried at 70°C for 96h) and leaf area (measured with a LiCor LI 3000 leaf area meter). Measurements were used to calculate specific leaf area (SLA, in m-2 leaf area g-1 dry weight) and leaf area index (LAI, in m2 leaf area m-2 floor area).

Harvest:

Fruit harvest started week 44, 6 weeks after planting. The number and weight of fruits was measured for five repetitions, each with two plants (compartment 1 and 2) to 9 plants in compartment 3 for each treatment. Ripened fruits, grade 8-9 on a scale from 1-12 (Bama AS), were harvested two times per week. Final destructive harvests were performed on 14 January 2019 on ten randomly selected plants for each treatment. All remaining fruits, leaves and stem were harvested for determination of fresh and dry weight (dried at 70°C for 96h) and leaf area (measured with a LiCor LI 3000 leaf area meter). Dry matter accumulation and distribution was calculated for plants at final harvest. Total dry matter production and distribution included dry matter of earlier harvested leaves and fruits.

Light use efficiency and energy use efficiency:

Light use efficiency (LUE: in gram (fresh weight of tomato fruits) per mol of photosynthetic photon) was calculated as the ratio between the cumulative yield of fresh tomatoes and the cumulative amount of photosynthetic photon received by the plants.
Energy use efficiency (in MJ kg-1 (fresh weight of tomato fruits)) was calculated as the ratio between the cumulative yield of fresh tomatoes (kg) per unit of cultivation area and the cumulative energy use in MJ per unit of cultivation area, consisting of heat energy, generated by a heating system used

for heating, electrical energy (PAR energy, thermal energy and conductive energy generated by lamps) consumed by lamps and solar energy, generated by the sun and received by plants in a greenhouse at plant height from the sun, from the start to the end of the harvesting period. Heat energy consumption per unit of cultivation area was measured using an energy flow meter (Kamstrup Multical 602). The electric energy consumption of installed lamps per unit of cultivation area was calculated from the amount of light installed in W m^{-2} and the number of hours where lamps were on. Global radiation was measured with a Kipp solarimeter, using a light transmission factor of 0.65 for the greenhouse cover.

Quality Analysis of Fruits:

Samples for fruit quality assessment were collected on 03.01.2019, 09.01.2019 and 14.01.2019. Each replicate consisted of six tomato fruits selected from the pool of fruits collected from ten plants for each individual treatment. Tomatoes with equal size and ripeness grade 8 were chosen for further analysis. Ripeness of the harvested fruits was determined visually by using a scale from 1 – green to 12 - deep red (provided by Bama AS).

At each date, three replicates (n=3) per treatment were prepared. Firmness was measured in scale from 1 to 100, where 100 - means full firmness and 1 - complete lack of firmness using a Durofel firmness tester (Agro Technologies, France). Each individual fruit within one replicate was measured at three locations on pericarp in the middle of fruit inner chambers. Thus, each replicate represents mean values of eighteen measurements (Verheul et al. 2015).

Samples for other quality tests were homogenized with a handheld blender to the uniform mixture. Prior homogenizations each tomato was cut on four parts. Six quarters (one quarter per fruit) were combined to make one replicate.

The fresh homogenized samples were used for estimation of soluble solid content (SSC) and total titratable acidity (TTA). Measurements of firmness, SSC and TTA were performed the same day as harvesting, following the procedures published by Mitcham and co-workers (Mitcham et al. 1996; Verheul et al. 2015).

Soluble solid content (expressed as °Brix) was measured with a digital refractometer PR-101α (ATAGO, Japan). Total titratable acidity was determined using an automatic titrator 794 Basic Titrino (Metrohm, Switzerland) and expressed as percent of citric acid equivalents (CAE) per FW.

Statistics:

Statistical differences in yield, plant characteristics and fruit quality parameters were evaluated using general linear model (ANOVA) followed by Turkey`s multiple comparisons test using Minitab 18 software (Minitab Ltd, UK).

RESULTS

Climatic conditions and water uptake

The average daily light integral received by the plants for the different treatments, including sunlight, is shown in Figure 2. Young tomato plants were planted on saturated rockwool slabs in the greenhouse in week 38. During establishing, plants received a maximum of 12 hours of HPS top light. This was gradually increased from 12 to 18 hours in week 41-44. In week 42, plants reached the level of the highest mounted of two LED lights, that were switched on in treatments 2,3,5 and 7. In week 43, two additional LED lights were switched on in treatment 3. The average DLI during harvesting (from week 44 - 2) received by the plants for treatments 1 to 7 was measured to be 20.2, 28.7, 37.3, 27.3, 35.9, 30.9 and 39.5 mol $m^{-2}d^{-1}$. This was very close to the planned DLI (Table 1). Of this, the amount of natural light at plant level was on average 1.7 mol $m^{-2}d^{-1}$, 6% of the total irradiation.

Figure 3 shows the climatic conditions during the establishing phase (week 38-43) and harvesting phase (week 44-2) in the three greenhouse compartments. Temperature was regulated optimal with regard to plant vigour. Stem diameter was used as a measure for plant vigour (Navarette et al., 1997), and temperature was regulated to keep a stem diameter in all treatments between 10 and 12 mm. During harvest, temperature was highest in the compartment with highest light intensity and lowest in the compartment with lowest light intensity in order to keep equal plant vigour in all three compartments.

The increase in the number of hours with HPS and switching on LED caused an increase in window opening and a moderate CO2 concentration in weeks 41-44 in all compartments. During harvesting, window opening gradually decreased and CO_2 concentration gradually increased in all compartments. Relative humidity was kept at a satisfactory level for plants between 60 and 85%.

Water uptake in liter per m2 and week was calculated from irrigation and drainage measurements in the three research compartments. Results show an increase in water uptake from planting to harvesting (Figure 4).

Yield and yield components

Results show clear effects of both HPS top light and LED inter-light on tomato yield and yield components (Table 2). On average, an increase in the installed amount of HPS top light from 161- to 242-Watt resulted in an increase in tomato yield of 53%. A further increase in HPS top light to 272 Watt had no significant effect on total yield. An increase in the installed amount of LED inter-light from 0 to 60 Watt resulted on average in a significant increase in yield ($p<0.05$). However, this increase in yield was 23% under 161-Watt HPS top light, but only 5 and 3% under 242- and 272-Watt HPS top light. A further increase in LED inter-light from 60- to 120-Watt under 161-Watt top light, increased yield with only 3%.

The increase in yield was strongly related to an increase in the number of harvested fruits, both at higher levels of HPS top light as well as higher levels of LED inter-light (Table 1). This was caused by both an increase in the number of trusses as well as an increase in the number of fruits per truss. Fruit weight was much less affected by the light treatments. An increase in HPS top light from 161 to 242 and 272 Watt installed, increased the number of harvested fruits on average with 68 and 92%. The number of trusses increased with 35 and 50%, while the number of fruits per truss was increased with 8 and 12 %. An increase in LED light from 0 to 60 and 120 in compartment 1, increased the number of harvested fruits with 13 and 20%. The number of trusses increased with 11 and 5%, while the number of fruits per truss was increased with 5 and 14 %.

Plant vigour and development

Some clear effects of light treatments on plant characteristics were observed (Table 3). An increase in HPS top light and LED inter-light had little effect on weekly plant length increase but reduced the distance between trusses. The reduced distance between trusses was related to a reduced fruit growth period ($r^2=0.84$). An increase in top light from 161 to 242 Watt resulted in an increased truss development rate with 12%, and increased weekly number of new fruits with 12%, a decrease in leaf length of 10% and a decrease in specific leaf area (SLA) of 32%. A further increase in top light had no effect on truss development rate, leaf length and SLA. Increase of LED inter-light tended however to reduce truss development rate and number of new fruits set on plants. LED inter-light decreased SLA with 12%.

Dry matter production and - distribution

Dry matter accumulation and distribution was measured on plants at final harvest. Calculation included dry matter of earlier harvested leaves and fruits. Results in Figure 5 show a quadratic polynomial relationship between the amount of installed light and total dry matter production (R^2 = 0.95). An increased amount of installed light had more effect on dry matter distribution to the fruits (R^2= 0.83) than on dry matter distribution to the leaves and stem (R^2= 0.93). Dry matter distribution to the fruits ranged from 51% at 161 Watt installed light to 61 % at 332 Watt installed light.

Fruit quality

Light treatments had significant effect on fruit quality (Table 4). Both an increase in the amount of HPS top-light and LED inter-light increased the content of soluble solids in the fruits. This increase was related to an increase in dry matter content of the fruits (R^2 = 0.9). Total titratable acidity (TTA) was not affected by light treatments. Fruit firmness decreased at higher amounts of HPS top light.

Light use efficiency

Light use efficiency (LUE: gram (fresh weight of tomato fruits) per mol of photosynthetic photon) was calculated as the ratio between the cumulative yield of fresh tomatoes and the cumulative amount of photosynthetic photon received by the plants in all treatments (Figure 6). Results show a lower LUE in all treatments with LED inter-light compared to LUE in all treatments without LED inter-light. Under 161 W top light, LUE decreased with 19 or 51% when 60- or 120-watt LED inter-light was added (Table 5). Under 242 and 272 W, LUE decreased with respectively 19 and 17% when 60 W LED inter-light was added.

An increase in HPS top light from 161- to 242-Watt, increased LUE with 6%. However, a further increase to 272 W decreased LUE with 18%.

Energy use efficiency

Energy use efficiency (in MJ kg^{-1}(fresh weight of tomato fruits)) was calculated as the ratio between the cumulative fresh tomato production (kg) and the cumulative energy use in MJ, consisting of heat energy, generated by a heating system used for heating, electrical energy (PAR energy, thermal energy and conductive energy generated by lamps and solar energy, generated by the sun and received by plants in a greenhouse at plant height, from the start to the end of the harvesting period. Results show that the energy use efficiency was inversely related to the light use efficiency and varied between 55 and 87 MJ kg^{-1} (Table 5). The treatment with 242 Watt installed HPS top light used less energy per kg tomato produced, while the treatment with 161 Watt installed HPS and 120 Watt installed LED was the least energy effective. The amount of heat energy used from planting to the end of the harvesting period was on average 4.2 MJ m^{-2} per week in all three compartments. This was only a small fraction of the total amount of energy. The total amount of energy needed from planting to start harvesting was 353, 432 and 490 MJ m^{-2} in compartments 1,2 and 3 respectively.

DISCUSSION

Methodology to compare effects of light conditions in the experiment

The impact of supplemental light on yield and yield components is strongly dependent on the regulation of other climate factors as well as crop management. Optimal tomato production in greenhouses and good greenhouse management requires a balance between light and temperature resulting in a balance between source and sink activities, i.e. assimilates availability and assimilate demand for growing organs (Stanghellini et al. 2019). In order to explain crop reactions to climate factors, we have tried to document both as good as possible.

In the present experiment, our aim was to optimize yield under different light conditions, while avoiding an unfavourable source-sink balance and reduce stress responses. We used stem thickness as a trait to regulate air temperature in the different greenhouse compartments. Earlier observations in tomato production using artificial light in Norway had shown that a stem diameter between 10 and 12 mm measured at plant height one week before, about 20 cm below shoot apex, resulted in a favourable source-sink balance and optimal yield. Results (Table 3) showed that we succeeded in our goal. As expected, an increase in the amount of light required an increase in air temperature to achieve the desired stem diameter. Optimization using stem diameter as a trait resulted in average temperatures during harvesting (week 44-2) of 20.8, 21.9 or 22.3 ^{o}C in the greenhouse compartments 1,2 or 3. At the start of the experiment, from planting to the start of the harvesting period, the strong vegetative growth required even higher air temperatures.

It is known that temperature has a large effect on all aspects of development. Leaf and truss initiation rates decrease linearly with decreasing temperature, while the period between anthesis and ripening of the fruit and fruit size increases (Adams et al., 2001; Van der Ploeg and Heuvelink, 2005). This is all confirmed in the present experiment.

Effects of HPS top light and LED inter-light on greenhouse climate

Earlier investigations have shown that HPS lamps emit a higher amount of radiation energy compared to LED lamps (Ouzounis et al., 2018). It can be expected that this will cause a higher transpiration from plants. Our results show a higher humidity in compartments with higher amount of HPS light installed especially during establishing (week 38-44). At a later stage during production, less differences in relative humidity were observed between compartments with different HPS light conditions. Water uptake was even reduced under higher amounts of HPS radiation during harvesting. This might suggest that plants have adapted to HPS radiation. The relative humidity during the experiment was kept between 60 and 85%. This is generally accepted as optimal for tomato production (Stanghellini et al., 2019).

The observed climatic conditions in the greenhouse give rise to a further optimisation of yield and energy use. The use of both HPS and LED lamps increase greenhouse air temperature, as shown by Verheul et al., 2020. In the present experiment, windows were opened due to a heat excess despite a low incoming solar radiation. This indicates that, even in winter, energy can be saved when the excess energy is harvested during the day and used during the night by using a heat exchanger (Righini et al, 2019). Furthermore, the reduction in window opening will increase the CO_2 concentration in the greenhouse air and thus support tomato production (Nederhoff, 1994, de Zwart, 2012).

<u>High pressure sodium top light and LED inter-light affect yield and yield components</u>

An increase in the installed amount of both HPS top light and LED inter-light increased plant productivity, biomass, the distribution of biomass to the fruits and fruit quality. The effect of additional LED inter-light was less at higher levels of HPS top light.

Tomato is recognised as a crop with a high light requirement. Under the conditions in the present experiment, the optimal daily light integral of HPS top light was shown to be around 30 mol. This confirms earlier assumptions (Moe et al., 2005). In general, every increment in PAR results in a comparable increase in tomato production (Marcelis et al., 2006). In the present experiment, an increase in installed HPS top light from 161 to 242 W m-2 increased yield with 53%. However, a further increase in HPS top light had no effect on yield. Differences in yield between different HPS top light treatments were mainly related to differences in the number of fruits and trusses and not to the average fruit weight. This implies that temperature regulation based on stem diameter in order to keep a satisfactory sink-source balance under higher amounts of HPS top light resulted in higher rates of plant development rather than a larger fruit size.

By adding extra light under equal temperature conditions, an increase in stem diameter might be expected. However, this was not the case when adding extra LED light as inter-light. In our previous investigations, we found a stronger effect of the supplemental LED on the mean weight of tomato fruits (Paponov et al., 2020). This indicates that LED intra-light stimulates generative growth rather than vegetative growth.

An installed amount of 60 W m^{-2} LED inter-light under 161 W m^{-2} HPS top light increased the yield with 23%. The main yield components contributing to this greater yield were an increase in the mean weight of the tomato fruits (6%) and an accelerated plant development, as indicated by the larger number of trusses per plant (11%) and an increase in the number of fruits per truss (5%). This is comparable to earlier observations under comparable conditions in a commercial greenhouse (Paponov et al, 2020). Results in the present experiment clearly show that the effect of LED light on yield and yield components is decreasing under increasing amounts of HPS top light. This indicates that, at higher light levels, other factors than light might be limiting for production. For example, earlier experiments have shown that tomato yield can further increase when higher plant densities, older plants at planting time, and/or higher CO_2 concentrations are used (Verheul et al., 2012).

A doubling in the amount of LED from 60 to 120 W m-2, or from two to four rows of inter-light, in the present experiment had only a minor effect on yield (3%) and yield components. It was earlier hypothesized that LED inter-light placed at a higher level in the plant, where fruits are in the stage of cell division (Bertin et al, 2002), will provide photo assimilates that might increase fruit cell division and thus increase fruit size (Paponov et al., 2020). However, no evidence of such was found in the present experiment.

Furthermore, it was shown that LED inter-light could not compensate for HPS top light. Plants receiving a DLI of 30 mol day^{-1} through HPS top light had 42% higher yield compared to plants receiving the same DLI with a combination of HPS top light and LED inter-light. Plants receiving an installed amount of top light of 272 W m-2 had 33% higher yield compared to plants receiving the same amount with a combination of HPS top light and LED inter-light, even though efficacy of LED light was higher than for HPS light.

Differences in yield results between HPS and LED lamps might partly be explained by their radiative properties and placement. HPS lamps generate high amounts of near infrared radiation energy when compared to LED lamps. This forces plants to evaporative cooling and opening of the stomata and might increase photosynthesis (Stanghellini et al, 2019). In contrast, LED lamps produces more convective heat that might lower relative humidity between the plants, forcing the plants to reduce stomatal opening and thus photosynthesis.

<u>High pressure sodium top light and LED inter-light affect plant vigour and generative/vegetative development</u>

Plant vigour and generative/vegetative development of plants can be affected by both light intensity and light quality. In young tomato plants, higher light intensity resulted in a reduced plant length increase, an increased stem diameter and a reduced specific leaf area (SLA) (Fan et al., 2013). The effect of light intensity on SLA was confirmed in the present experiment for both HPS top light and LED inter-light. Increased LED inter-light reduced plant length increase. However, the effect of HPS top light on plant length was less clear. This was probably caused by the experimental set-up where these effects were reduced by using a higher growth temperature. Higher top light intensities combined with higher temperatures resulted in comparable plant length increase and an increased truss development rate and thus shorter distances between trusses. These conditions also decreased the fruit growth period and increased the allocation of dry matter to the fruits. It appears that the sink limitation, that might be expected with higher light intensities, was reduced by using higher temperatures.

Studies on effects of light quality in tomato have shown that light spectral and thermal properties affect biomass allocation among plant parts during tomato growth and development (Kim et al., 2019). This study showed that LED supplemented plants allocated more dry mass to the fruits, while HPS supplemented plants allocated a higher fraction of total biomass to vegetative tissues. In the present experiment, where much higher light intensities were used, it is shown that increased light intensity increased dry mass allocation to the fruits both under LED and HPS light.

High pressure sodium top light and LED inter-light affect fruit quality

The soluble solid content (SSC), and the ratio between SSC and the total titratable acidity (TTA) are key quality parameters for tomato quality (Verheul, 2015). Earlier investigations have shown that these quality parameters can be influenced by both light intensity (Slimestad and Verheul, 2005; Pan et al., 2019) and light spectral and thermal properties (Kim et al., 2019). Kim et al. (2020) concluded that HPS lamp-supplemented tomatoes had less nutritional and overall sensory profiles compared to LED lamp supported tomatoes as explained by the direct irradiation to developing fruits with intra canopy LED's. The present experiment shows that both a higher amount of installed HPS top-light and LED inter-light increased the SSC while TTA was not affected. Apparently, the conditions in the present experiment that increased allocation of dry matter to the fruits, also increased the dry matter content and SSC in the fruits. Tomato quality, as expressed by SSC/TTA appeared to be more related to light intensity than to light quality and its distribution along the canopy.

Light use efficiency of different amounts of HPS top light

A linear relationship between fresh or dry mass production (g) and the cumulative intercepted sum of photosynthetic photon (mol m^{-2}) has been observed for many crops. The slope of this relationship is called the crop light use efficiency (LUE) (Heuvelink and Dorais, 2005). LUE determines how much production is realized per unit of intercepted light and takes in account the process of gross photosynthesis and respiration without detailing them. For field crops, sown and harvested during a growing season, LUE is assumed to be constant (Stanghellini et at, 2019). In a greenhouse, LUE depends on the light level, the environmental temperature and variation in 24h, the CO_2 concentration during the day, relative humidity, the fraction of absorbed light, the leaf area index, the sink source ratio and the harvest index. Thus, under the given environmental conditions in winter for the specific crop, LUE is a good measure to characterize the effects of different types of artificial light on plant production (Cocetta et al, 2017, Kozai, 2018). The most efficient use of artificial light will occur when a high LUE is combined with a high yield. A reduction in LUE occurs at light levels close to light saturation or at otherwise less than optimal crop growing conditions.

During the harvesting period in the present experiment, light from the sun was minimal, giving us a unique possibility to assess the light use efficiency for artificial light only. In this experiment, with the given environmental and plant conditions, the most efficient use of artificial light occurred under 242 Watt installed HPS top light. A further increase in the amount of HPS top light reduced LUE, indicating that light levels were closer to saturation under the given conditions. Also, a lower amount of HPS top light resulted in a lower LUE. Under the present environmental conditions, with optimal temperature, CO2 concentration and relative humidity and a fraction of absorbed light of 97%, the lower LUE might be related to a lower rate of gross photosynthesis, a higher rate of respiration and/or the lower observed harvest index.

A maximum LUE of 10.34 g FW mol-^{1} was measured in the treatment with 242 Watt installed top light. Higashide and Heuvelink (2009) showed LUE of modern tomato cultivars are around 12.5 g FW mol^{-1} . This might indicate that the optimum LUE is still not reached in the present experiment. Earlier experiments have shown that yield can be further increased by increasing plant density and the age of plants at planting time (Verheul, 2012).

Light use efficiency of LED inter-light

Addition of LED inter-light increased yield, but reduced LUE. This indicates that LED inter-light was used less efficient in gross photosynthesis. The reduction in LUE was approximately the same in all cases where 60 W LED inter-light was added: 19, 19 or 17% respectively in compartment 1,2 or 3, whereas the increase in yield was 23, 5 or 3 %. Comparable results were achieved in earlier experiments (Paponov et al., 2020). The reduction in LUE when adding LED inter-light might be caused by situation closer to light saturation. However, comparable amounts light given by a combination of HPS and LED or HPS top-light only, when comparing treatments 2 and 4 or 3 and 5, resulted in a higher LUE for HPS top light only. Under the given conditions, it can be concluded that HPS top light was more effective to increase yield compared to LED inter-light.

It should be considered that the smaller effects of LED inter-light at higher levels of HPS top light might indicate that, in these cases, other factors than light have become a minimum factor. Since plant vigour, vegetative / generative development and harvest index were related to the amount of light installed, climatic factors like air temperature, relative humidity and/or CO_2 concentration in the air might be these limiting factors. The fact that temperature is one of these factors is confirmed by the observation that comparable amounts of light at higher temperatures gives higher values of LUE (compare treatment 2 and 4 or 3 and 5). This is also in line with earlier observations in summer production (Verheul et al., 2020). It can be concluded that the effects of LED inter-lighting on plant productivity depend on top light intensity as well as on other environmental conditions. In the present experiment we have chosen to compare effects of light for one genotype and plant density. It might be expected that the optimal situation will be different for different genotypes, plant densities and fruit / leaf ratios.

Energy use efficiency and environmental load

The main energy components in greenhouse production in northern Europe are sunlight as well as natural gas and electricity for heating and lighting (Baptista et al., 2013). In a reference standard tomato crop in the Netherlands with a growing season of 11 months producing 60 kg m-2, 4319 MJ m-2 energy enters the greenhouse, of which 65% originated from solar radiation and 35% from heating using natural gas, total energy use is calculated to be 72 MJ kg-1 FW (Elings et al., 2005). In a winter production of tomatoes in the Netherlands, from 15th October to 1st of July, using an HPS LED hybrid system, an energy use of 125 MJ kg-1 was calculated by Dueck et al. (2012). A reference tomato crop in Spain yields 16.5 kg m-2 a year (Montero et al., 2011) and receives about 4200 MJ m-2 solar radiation, resulting in an energy use of 255 MJ kg-1. Compared to the results of our experiment in Norway, with an energy use of only 55-75 MJ kg-1, it can be concluded that winter production in Norway under artificial light is more energy effective compared to production under efficient production conditions under sunlight in more southern countries.

The use of natural gas for heating is the main cause for CO_2 emissions from tomato and cucumber production in northern Europe (Verheul and Thorsen, 2010). Tomato production in the Netherlands, using about 7 kWh of natural gas per kilo tomato and a CO_2 emission of 0,273 kg kWh-1 (Moreno

Ruiz et al., 2018), causes a CO_2 emission of 1.9 kg CO_2 equivalents per kilo tomato for gas only. Results from the present experiment showed that the energy needed for heating in winter production in Norway is only 0.6 kWh kg-1, due to the high amounts of installed supplemental light. If natural gas is used for heating in Norway, this corresponds to a CO_2 emission of 0.4 kg CO_2 eq. per kilo tomato produced. This is equal to the CO_2 emission of tomatoes produced in Spain (Torellas et al., 2012). Both sunlight and hydroelectric energy are renewable energy sources. Unlike sunlight, hydroelectric energy, commonly used in Norway, is not for free, which makes production in Norway more expensive.

In conclusion, it was confirmed that supplemental HPS top light and LED inter-light increased tomato yield. However, the positive effect of supplemental LED inter-light on yield decreased at higher amounts of HPS top light. Under the experimental conditions with neglectable incoming solar radiation, an installed amount of 242 Watt m-2 HPS top light resulted in best light use efficiency (in gram fresh product per mol photosynthetic photon). The addition of LED inter light to HPS top light reduced light use efficiency but increased fruit size and quality. Results show that winter production by using artificial light in Norway is more energy efficient compared to production under sunlight in more southern countries. These results can be used for modelling purposes.

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REFERENCES

Adams, S.R., Cockshull, K.E. and Cave, C.R.J. (2001). Effects of temperature on the growth and development of tomato fruits. Ann. Bot. 88, 869-877 https://doi.org/10.1006/anbo.2001.1524

Baptista, F.J, Briassoulis, D., Stanghellini C., Silva, L.L, Balafoutis A.T, Meyer-Aurich, A., Mistriotis, A. (2013). Energy efficiency in tomato greenhouse production. A preliminary study. ISHS Acta Horticulturae 1037: International Symposium on New Technologies for Environment Control, Energy-Saving and Crop Production in Greenhouse and Plant Factory - Greensys 2013 DOI: 10.17660/ActaHortic.2014.1037.18

Bertin, N., Gautier, H., and Roche, C. (2002). Number of cells in tomato fruit depending on fruit position and source-sink balance during plant development. Plant Growth Regul. 36, 105–112. doi: 10.1023/a:1015075821976

Bugbee, B., 2016. Toward an optimal spectral quality for plant growth and development: the importance of radiation capture. Acta Hortic. 1134, 1–12.

Cocetta, G., Casciani, D., Bulgari, R. et al. Light use efficiency for vegetables production in protected and indoor environments. Eur. Phys. J. Plus 132, 43 (2017). https://doi.org/10.1140/epjp/i2017-11298-x.

Davis, P.A., and Burns, C. (2016). Photobiology in protected horticulture. Food and Energy Security 2016; 5(4): 223–238 doi: 10.1002/fes3.97

De Koning, A.N.M. (1994). Development and dry matter distribution in glasshouse tomato: a quantitative approach. PhD-thesis Wageningen University, the Netherlands, 227 pp. ISBN 90-5485-332-8.

De Kreij, C., Voogt, W. and Baas, R. (1999) Nutrient solutions and water quality for soilless cultures. Brochure 196. Research Station for Floriculture and Glasshouse Vegetables (PBG), Naaldwijk, The Netherlands, 32 pp

De Visser, P.H.B. Buck-Sorlin, G.H and van der Heijden, G.W.A.M (2014). Optimizing illumination in the greenhouse using a 3D model of tomato and a ray tracer. Front. Plant Sci., 18 February 2014 | https://doi.org/10.3389/fpls.2014.00048

De Zwart (2012). Lessons learned from experiments with semi-closed greenhouses. Acta Hort. 952: 583-588.

Dieleman JA, De Visser PHB, Meinen E, Grit JG and Dueck TA (2019) Integrating Morphological and Physiological Responses of Tomato Plants to Light Quality to the Crop Level by 3D Modeling. Front. Plant Sci. 10:839. doi: 10.3389/fpls.2019.00839

DLC, The DesignLights Consortium (2021). www.designlights.org

Dorais, M (2003). The use of supplemental lighting for vegetable crop production: light intensity, crop response, nutrition, crop management, cultural practices. Canadian Greenhouse Conference, Toronto, Ontario, [Canada]; October 9, 2003.

Dueck, T.A, Janse J., Eveleens B.A, Kempkes F.L.K and Marcelis, L.F.M (2012). Growth of Tomatoes under Hybrid LED and HPS Lighting. Proc. IS on GreenSys2011. Eds.: C. Kittas et al. Acta Hort. 952, ISHS 2012, 335-342.

Dzakovich, M.P., Gomez, C. and Mitchell, C.A. (2015). Tomatoes Grown with Light-emitting Diodes or High-pressure Sodium Supplemental Lights have Similar Fruit-quality Attributes. HortScience 50 (10): 1498-1502. https://doi.org/10.21273/HORTSCI.50.10.1498

Elings, A., Kempkes, F.L.K., Kaarsemaker, R.C, Ruijs, M.N.A, van de Braak N.J., and Dueck, T.A. (2005). The Energy Balance and Energy-Saving Measures in Greenhouse Tomato Cultivation. Proc. IC on Greensys. Eds.: G. van Straten et al. Acta Hort. 691, ISHS 2005, 67-74. DOI: 10.17660/ActaHortic.2005.691.5 · Source: OAI

Fan, X-X., Xu, Z-G., Liu, X-Y., Tang, C-M., Wang, L-W., Han, X-L. (2013). Effects of light intensity on the growth and leaf development of young tomato plants grown under a combination of red and blue light. Scientia Horticulturae Volume 153 (4) : 50-55. https://doi.org/10.1016/j.scienta.2013.01.017

Gajc-Wolska, J, Kowalczyk, K, Metera, A, Mazur, K. Bujalski D., Hemka, L. (2013). Effect of supplementary lighting on selected physiological parameters and yielding of tomato plants. Folia Hort. 25/2 (2013): 153-159 DOI: 10.2478/fhort-2013-0017

Gerganova, M., Popova, A.V., Stanoeva, D. and Velitchkova M. (2016). Tomato plants acclimate better to elevated temperature and high light than to treatment with each factor separately. Plant Physiology and Biochemistry 104 (2016) 234-241.

Gierson D., Kader A.A. (1986) Fruit ripening and quality. In: Atherton J.G., Rudich J. (eds) The Tomato Crop. The Tomato Crop (A scientific basis for improvement). Springer, Dordrecht. https://doi.org/10.1007/978-94-009-3137-4_6

Gislerød, H.R, Mortensen, L-M, Torre, S., Pettersen, H., Dueck, T., Sand, A. (2012). Light and energy saving in modern greenhouse production. ISHS Acta Horticulturae 956: VII International Symposium on Light in Horticultural Systems. DOI: 10.17660/ActaHortic.2012.956.7

Gomez, C., and Mitchell, C. A. (2016). Physiological and productivity responses of high-wire tomato as affected by supplemental light source and distribution within the canopy. J. Am. Soc Hortic. Sci. 141, 196–208. doi: 10.21273/JASHS.141.2.196

Heuvelink, E. and Dorais, M. (2005). Crop growth and yield. In: Tomatoes, Ed. E. Heuvelink. CAB International 2005.

Heuvelink, E, Bakker, M.J, Hogendonk, L., Janse, J., Kaarsemaker, R. Maaswinkel, R. (2006). Horticulturel lighting in the Netherlands: New developments. ISHS Acta Horticulturae 711. https://doi.org/10.17660/ActaHortic.2006.711.1

Heuvelink, E. (ed) (2018). Tomatoes, 2nd edition. Crop Production Science in Horticulture. CABI, Wallingford, UK, 256 pp.

Highashide, T., Heuvelink., E. (2009). Physiological and Morphological Changes Over the Past 50 Years in Yield Components in Tomato. HortSci 134 (4): 460-465. https://doi.org/10.21273/JASHS.134.4.460

Hogewoning, S.W., Trouwborst, G., Maljaars, H., Poorter, H., van Ieperen, W., Harbinson, J. (2010). Blue light dose–responses of leaf photosynthesis, morphology, and chemical composition of Cucumis sativus grown under different combinations of red and blue light. J. Exp. Botany 61, (11): 3107–3117. https://doi.org/10.1093/jxb/erq132

Kader, A. A.; Morris, L. L.; Stevens, M. A.; Albright-Holton, M. (1978). Composition and flavor quality of fresh marked tomatoes as influences by some postharvest handling procedures. J. Am. Soc. Hortic. Sci. 1978,103, 6−13.

Kaiser E, Ouzounis T, Giday H, Schipper R, Heuvelink E and Marcelis LFM (2019) Adding Blue to Red Supplemental Light Increases Biomass and Yield of Greenhouse-Grown Tomatoes, but Only to an Optimum. Front. Plant Sci. 9:2002. doi: 10.3389/fpls.2018.02002

Kim, H.J, Lin, M-Y and Mitchell C.A (2019). Light spectral and thermal properties govern biomass allocation in tomato through morphological and physiological changes. Environmental and Experimental Botany. Volume 157, January 2019, Pages 228-240. doi.org/10.1016/j.envexpbot.2018.10.019

Kim, H.J, Yainga, T., Choia, S., Wanga, Y., Lina, M.Y and Liceagab, A.M. (2020). Supplemental intracanopy far-red radiation to red LED light improves fruit quality attributes of greenhouse tomatoes. Sci. Hort. 261 (2020) 108985. doi.org/10.1016/j.scienta.2019.108985

Kozai, T. (2018). Smart Plant Factory: The Next Generation Indoor Vertical Farms. Springer, Singapore. doi: 10.1007/978-981-13-1065-2

Körner, O., Heuvelink, E. and Niu, Q (2009). Quantification of temperature, CO2, and light effects on crop photosynthesis as a basis for model-based greenhouse climate control. Journal of Horticultural Science & Biotechnology (2009) 84 (2) 233–239

Li, T., Heuvelink, E., and Marcelis, L.F.M. (2015). Quantifying the source-sink balance and carbohydrate content in three tomato cultivars. Frontiers in Plant Science 6: 416 https://doi.org/10.3389/fpls.2015.00416

Marcelis, L.F.M, Broekhuijsen, A.G.M., Nijs, E.M.F.M, and Raaphorst, M.G.M. (2006). Quantification of the growth response of light quantity of greenhouse-grown crops. Acta Hort 711: 97-104 https://doi.org/10.17660/ActaHortic.2006.711.9

McCree, K. J., 1972. The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. Agric. Meteorol, 9: 191-216.

Mitcham, B.; Cantwell, M.; Kader, A. (1996). Methods for determining quality of fresh commodities. Perishables Handling Newsletter 1996, 85, 1−5.

Moe, R., Grimstad, S.O, and Gislerød, H.R. (2005). The use of artificial light in year-round production of greenhouse crops in Norway. https://doi.org/10.17660/ActaHortic.2006.711.2

Moerkens, R., W. van Lommel, R. Vanderbruggen and van Delm, T. (2016). The added value of LED assimilation light in combination with high pressure sodium lamps in protected tomato crops. Acta Horticulturae 1134: 119-124. https://doi.org/10.17660/ActaHortic.2016.1134.16

Montero JI, Antón A, Torrellas M, Ruijs M, Vermeulen P (2011). Report on environmental and economic profile of present greenhouse production systems in Europe. European Commission. FP7-KBBE-2007–1 Project EUPHOROS (Reducing the need for external inputs in high value protected horticultural and ornamental crops). http://www.euphoros.wur.nl/UK

Moreno Ruiz, E, L Valsasina, F Brunner, A Symeonidis, D FitzGerald, K Treyer, G Bourgault, and G

Wernet (2018). \Documentation of changes implemented in ecoinvent database v3. 5". In: Ecoinvent: Zürich, Switzerland.

Navarette, M., Jannequin, B. and Sebillotte, B. (1997) Vigour of greenhouse tomato plants (*Lycopersicon esculentum* Mill.): Analysis of the criteria used by growers and search for objective criteria. Journal of Horticultural Science 72 (5): 821-829. DOI: 10.1080/14620316.1997.11515576

Nederhoff, E.M. (1994). Effects of CO2 concentration on photosynthesis, transpiration and production of greenhouse vegetable crops. PhD-thesis Wageningen University, the Netherlands, 227 pp. ISBN 9789054853183 – 213.

Nelson, J.A., Bugbee, N. (2014). Economic Analysis of Greenhouse Lighting: Light Emitting Diodes vs. High Intensity Discharge Fixtures. PLoS ONE 9(6): e99010. https://doi.org/10.1371/journal.pone.0099010

Ouzounis, T., Giday, H., Kjaer, K.H., and Ottosen, C.-O. (2018). LED or HPS in ornamentals? A case study in roses and campanulas. Eur. J. Hortic. Sci. 83(3), 166–172. doi.org/10.17660/eJHS.2018/83.3.6

Pan,T., Ding, J., Qin,G., Wang, Y., Xi,L., Yang, J., Li, J., Zhang, J., and Zou, Z. (2019). Interaction of Supplementary Light and CO2 Enrichment Improves Growth, Photosynthesis, Yield, and Quality of Tomato in Autumn through Spring Greenhouse Production. HortScience 54(2):246–252. 2019. https://doi.org/10.21273/HORTSCI13709-18

Paponov, M., Verheul, M.J and Paponov I.A. (2018). LED inter-lighting increases tomato yield due to the higher photosynthetic light use efficiency of low-positioned leaves. 1st European Congress on Photosynthesis Research, Uppsala, 25.06.2018-28.06.2018.

Paponov, M., Kechasov D., Lacek, J., Verheul, M.J and Paponov, I.A (2020). Supplemental Light-Emitting Diode Inter-Lighting Increases Tomato Fruit Growth Through Enhanced Photosynthetic Light Use Efficiency and Modulated Root Activity. Front. Plant Sci. 10:1656. doi: 10.3389/fpls.2019.01656

Peet and Welles (2005). In: Tomatoes, Ed. E. Heuvelink. CAB International 2005.

Persoon, S. and Hogewoning, S.W (2014). Onderzoek naar de fundamenten van energiebesparing in de belichte teelt Productschap Tuinbouw (2014), pp. 16-18. https://www.kasalsenergiebron.nl/content/research/14764.04_Fundamenten_energiebesparing_belichte_teelt.pdf

Pettersen, R.I, Torre, S. and Gislerød, H.R (2010). Effects of leaf aging and light duration on photosynthetic characteristics in a cucumber canopy. Scientia Horticulturae 125 (2), 82-87. doi.org/10.1016/j.scienta.2010.02.016

Righini, I., Vanthoor, B., Verheul, M.J., Naseer, M., Maessen, H., Persson, T., Stanghellini, C. (2020). A greenhouse climate-yield model focusing on additional light, heat harvesting and its validation Biosystems Engineering 194: 1-15. https://doi.org/10.1016/j.biosystemseng.2020.03.009

Sarlikioti, V., de Visser, P.H.B., Buck-Sorlin, G.H., Marcelis, L.F.M., 2011. How plant architecture affects light absorption and photosynthesis in tomato: towards an ideotype for plant architecture using a functional - structural plant model. Ann. Bot. 108, 1065–1073.

Slimestad, R. and Verheul, M.J. (2005) Seasonal Variations in the Level of Plant Constituents in Greenhouse Production of Cherry Tomatoes J. Agric. Food Chem. 2005, 53, 8, 3114–3119 https://doi.org/10.1021/jf047864e

Stanghellini, C., van 't Ooster, A., and Heuvelink, E., 2019. Greenhouse horticulture. Technology for optimal production. Wageningen Academic Publishers, The Netherlands, 2019. ISBN 978-90-8686-329-7.

Stevens, M. A.; Kader, A. A.; Albright-Holton, M.; Algazi, M. (1977). Genotypic variation of flavor and composition in fresh market tomatoes. J. Am. Soc. Hortic. Sci. 1977, 102, 680−689.

Sun, J., Nishio, J.N., Vogelmann, T.C., 1998. Green light drives CO2 fixation deep within leaves. Plant Cell Physiol. 39, 1020–1026.

Thimijan, R.W, and Heins, R.D. (1983). Photometric, radiometric and quantum light units of measure: a review of procedures for interconversion. HortScience 18: 818-822.

Torrellas, M., Antón, A., López, J.C, Baeza, E.J, Pérez Parra J., Muñoz P. and Montero, J.I (2012). LCA of a tomato crop in a multi-tunnel greenhouse in Almeria. Int J Life Cycle Assess. DOI 10.1007/s11367-012-0409-8

Trouwborst, G., Hogewoning, S. W., Harbinson, J., and Van Ieperen, W. (2011). The influence of light intensity and leaf age on the photosynthetic capacity of leaves within a tomato canopy. J. Hortic. Sci. Biotech. 86, 403–407. doi: 10.1080/14620316.2011.11512781

Vadiee, A. and Martin. V. (2012). Energy management in horticultural applications through the closed greenhouse concept, state of the art. Renewable and Sustainable Energy Reviews 16 (7): 5087-5100 https://doi.org/10.1016/j.rser.2012.04.022

Van der Ploeg, A., Heuvelink, E. (2005). Influence of sub-optimal temperature on tomato growth and yield: a review. Horticultural Science and Biotechnology 80 (2005) 6: 652-659. https://doi.org/10.1080/14620316.2005.11511994

Verheul, M.J and Thorsen S.M. (2010). Klimagassregnskap for norske veksthusprodukter. Bioforsk Rapport 5: 135 (2010), 81 pp.

Verheul, M.J. (2012). Effects of plant density, leaf removal and light intensity on tomato quality and yield. Acta Hort 956: 389-394. https://doi.org/10.17660/ActaHortic.2012.956.42

Verheul, M.J., Maessen, H.F.R, Grimstad, S.O. (2012). Optimizing a year-round cultivation system of tomato under artificial light. Acta Hort 956: 389-394 https://doi.org/10.17660/ActaHortic.2012.956.45

Verheul, M.J., Slimestad, R. and Holta Tjøstheim, I. (2015) From Producer to Consumer: Greenhouse Tomato Quality As Affected by Variety, Maturity Stage at Harvest, Transport Conditions, and Supermarket Storage. J. Agric. Food Chem. 2015, 63, 20, 5026–5034 https://doi.org/10.1021/jf505450j

Verheul, M.J., Maessen, H.F.R., Panosyan, A., Naseer, M., Paponov, M. and Paponov, I.A. (2020). Effects of supplemental lighting and temperature on summer production of tomato in Norway. Acta Hortic. 1296, 707-714 DOI: 10.17660/ActaHortic.2020.1296.89

Watada, A. E.; Aulenbach, B. E. Chemical and sensory qualities of fresh market tomatoes. J. Food Sci. 1979, 44, 1013−1016.

Yan, W., Zhang, Y., Zhang, Y., Cheng, R., Zhang, Y., Yang, Q. and Li, T. (2018). Effects of supplementary artificial light on growth of the tomato (*Solanum Lycopersicum*) in a Chinese solar greenhouse. The Horticultural Journal 87 (2018) 4: 516-523. https://doi.org/10.2503/hortj.OKD-165

Zhen, S. and Bugbee, B. (2020). Far-red photons have equivalent efficiency to traditional photosynthetic photons: Implications for redefining photosynthetically active radiation. Plant Cell Environ. 2020; 43:1259–1272. DOI: 10.1111/pce.13730

Figures

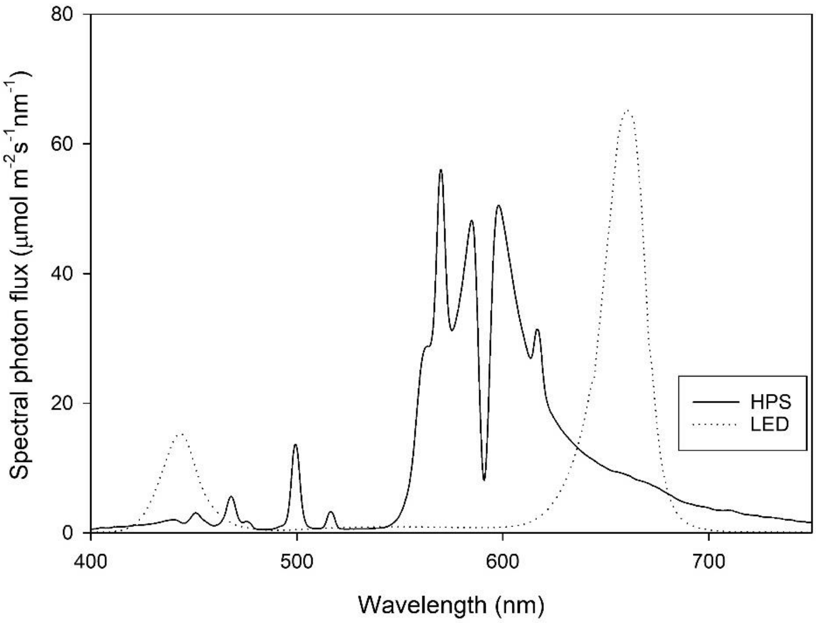

Figure 1. Spectral distributions of High Pressure Sodium (HPS) and Light Emitting Diode (LED) lamps used in the experiment.

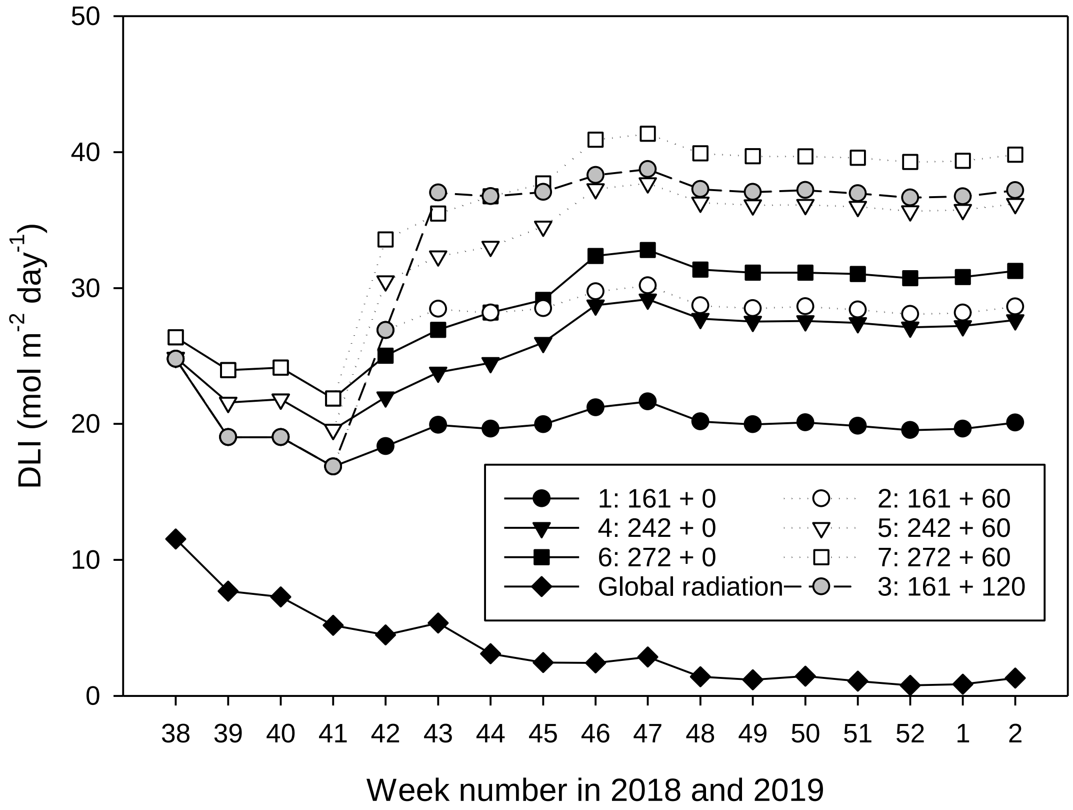

Figure 2: Light conditions at plant level in the greenhouse. Weekly average for the daily light integral (DLI) for natural irradiance (Global radiation) and light treatments (1-7) with high pressure sodium top-light (161, 242 and 272 W m^{-2} installed) and light-emitting diode inter-lighting (0, 60, 120 W m^{-2} installed)

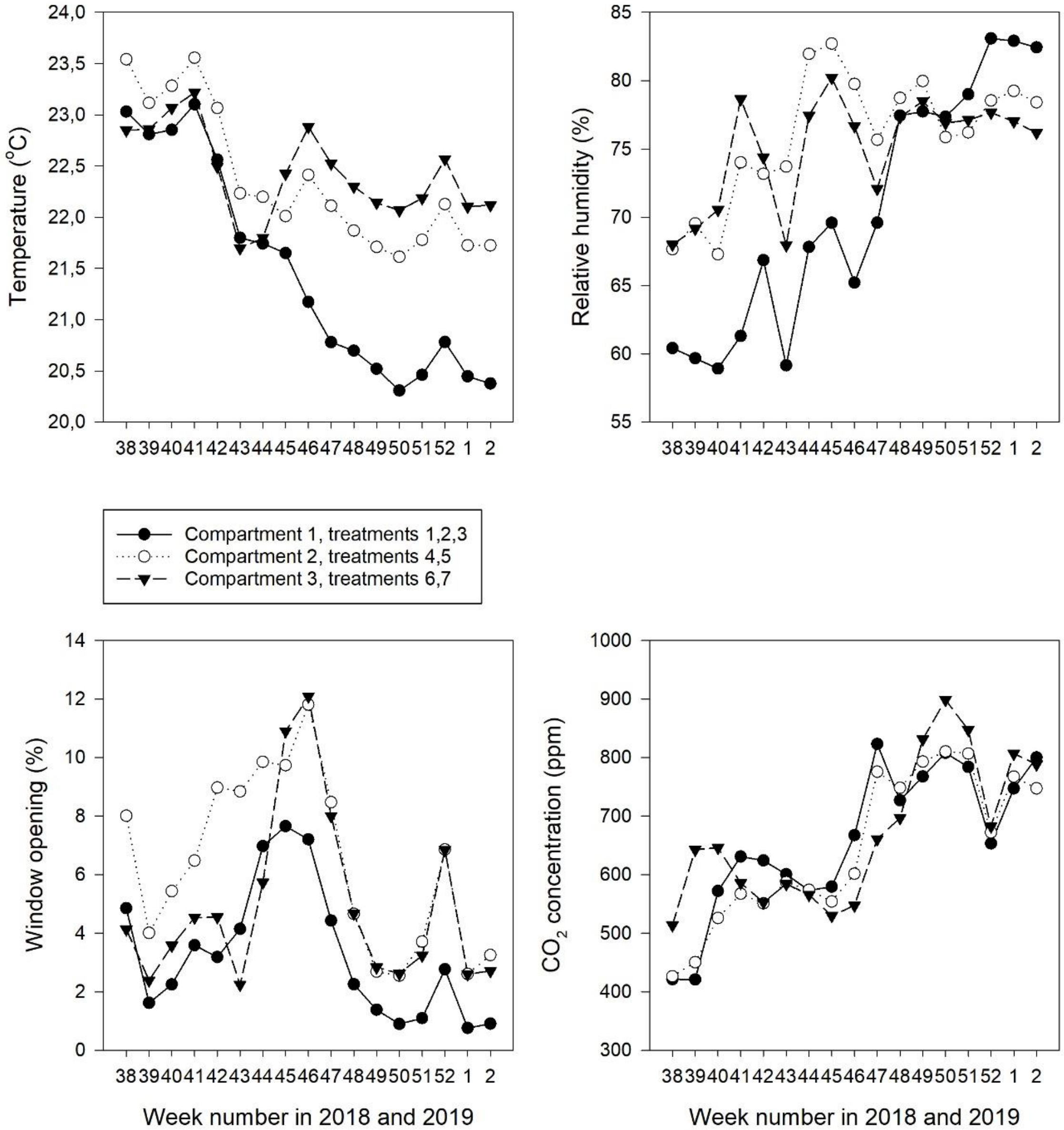

Figure 3: Weekly averages for temperature (oC), relative air humidity (%), ventilation opening (%) and CO2 concentration in the air (ppm) in three greenhouse compartments and light treatments (1-7) during the experiments.

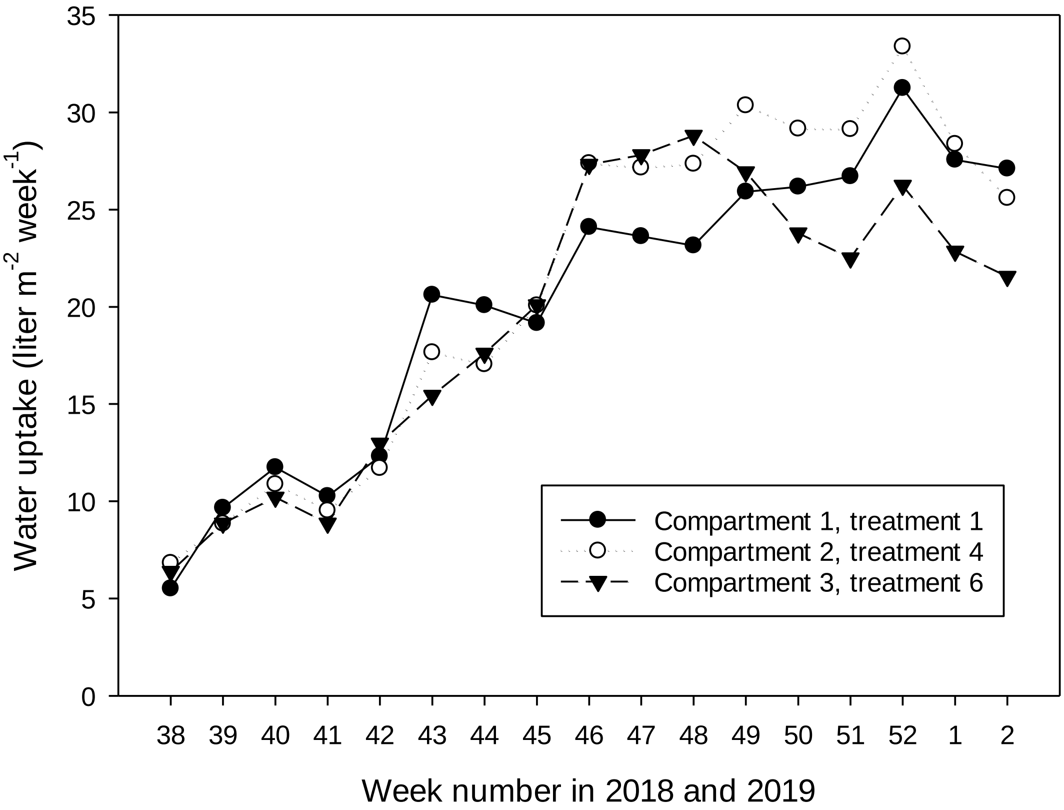

Figure 4: Weekly summarized water uptake (l m^{-2}) in three greenhouse compartments during the experiments.

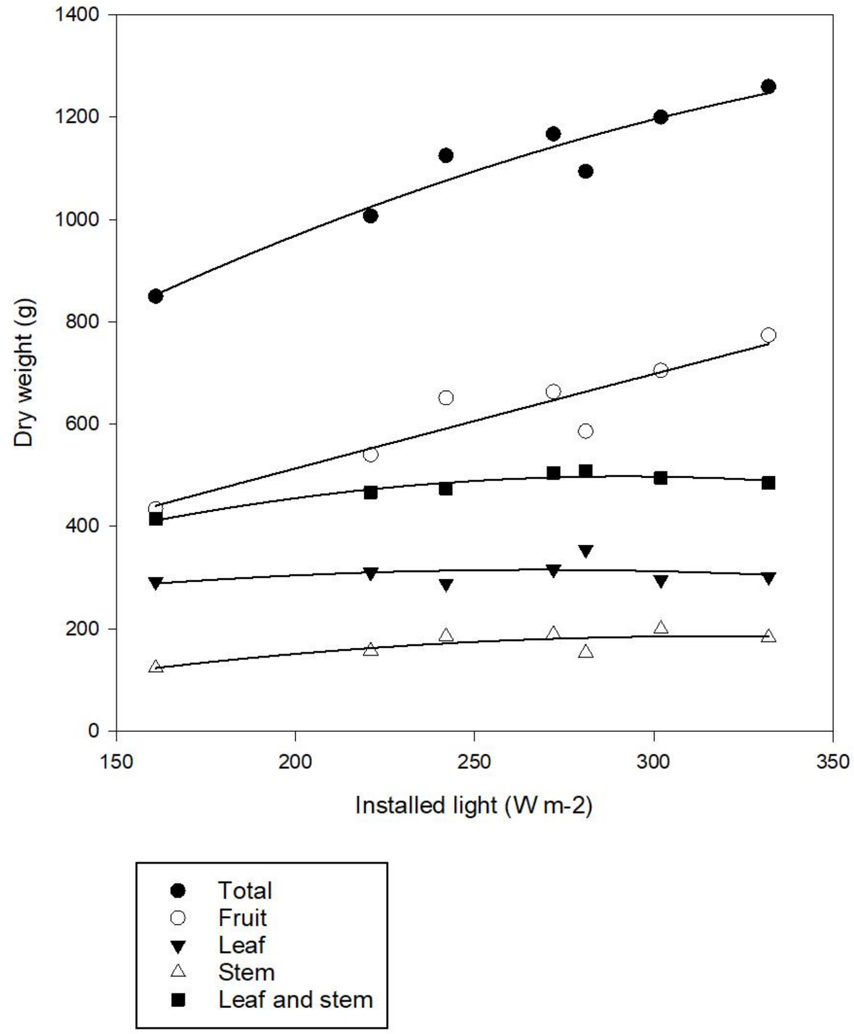

Figure 5: Total dry matter accumulation and distribution to fruits, leaves and stem in tomato plants at final harvest (in g) as a function of the total installed amount of artificial light (in W m-2).

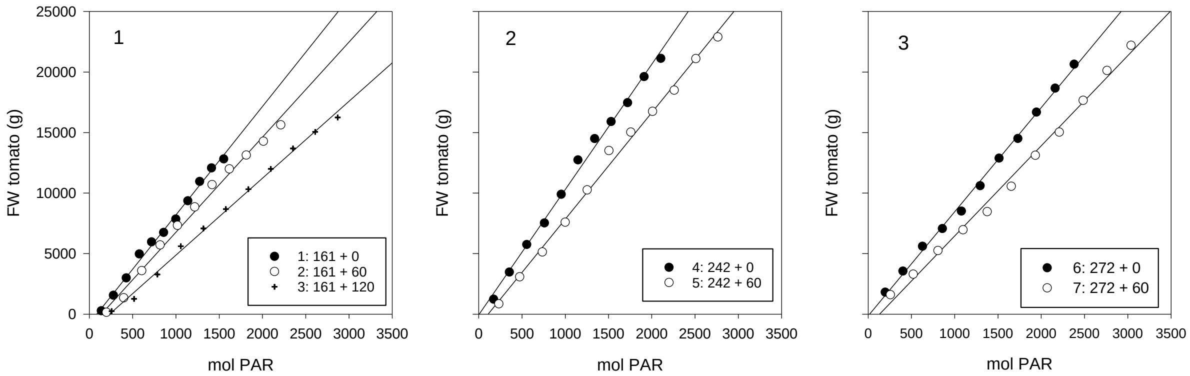

Figure 6: Efficiency of use of HPS top light (161, 242 or 272 W m-2 installed) and LED inter-light (0, 60 or 120 W m-2 installed) for light treatments 1-7. The y- axis shows cumulated fresh tomato yield (g) and the x-axis shows cumulated artificial and solar radiation (mol Photosynthetic Photon (PP)) received by the plants. Each point is one harvesting week (two harvesting events). The slope of the best-fit lines is the light use efficiency of the growing system (data and R^2 in Table 5).

Table 1: Overview of light treatments with HPS top light and LED inter light used during the experiment.

Treatment	Greenhouse compartment	Top light HPS W m^{-2} installed	Inter light LED W m^{-2} installed	PPFD µmol $m^{-2}s^{-1}$ *	DLI mol $m^{-2}d^{-1}$ *
1	1	161	0	290	18.8
2	1	161	60	422	27.3
3	1	161	120	554	35.9
4	2	242	0	436	28.2
5	2	242	60	566	36.8
6	3	272	0	490	31.7
7	3	272	60	622	40.3

* Photosynthetic Photon Flux Density (PPFD, in µmol m-2s-1) and the daily light integral (DLI, mol m-2d-1) were calculated based on a day length of 18 h per day (06:00-24:00) and a light efficacy of 1.8 and 2.2 µmol J-1 for HPS and LED lamps, respectively.

Table 2. The effects of supplemental HPS top light and LED inter-light (in Watt m^{-2} installed) on yield, fruit weight, number and distance of trusses, and number of fruits per truss at final harvest.

Traits	Treatments	1	2	3	4	5	6	7
	Compartment		1		2		3	
	HPS toplight (W m^{-2})	161	161	161	242	242	272	272
	LED inter-light (W m^{-2})	0	60	120	0	60	0	60
Total yield (kg m^{-2})		12.8 (c)	15.8 (b)	16.3 (bc)	21.4 (a)	22.5 (a)	21.6 (a)	22.3 (a)
Number of harvested fruits ($plant^{-1}$)		53 (c)	62 (c)	63 (c)	83 (b)	86 (b)	93 (ab)	99 (a)
Average fruit weight (g)		80 (abc)	85 (ab)	86 (ab)	86 (ab)	87 (a)	77 (bc)	75 (c)
Number of trusses harvested ($plant^{-1}$)		9.1 (b)	10.1 (ab)	9.6 (b)	12.7 (ab)	13.3 (ab)	14.4 (a)	14.3 (a)
Number of fruits per truss		5.8 (b)	6.1 (b)	6.6 (ab)	6.5 (ab)	6.5 (ab)	6.5 (ab)	6.9 (a)
Number of trusses not harvested ($plant^{-1}$)		10.6 (a)	10.0 (a)	10.4 (a)	9.2 (b)	9.2 (b)	10.1 (a)	10.7 (a)

Table 3: The effects of HPS top light and LED inter-light on plant vigour and vegetative/generative development.

Traits	Treatments	1	2	3	4	5	6	7
	Compartment		1		2		3	
	HPS toplight (W m^{-2})	161	161	161	242	242	272	272
	LED inter-light (W m^{-2})	0	60	120	0	60	0	60
Plant length increase (cm $week^{-1}$)		22.6 (ab)	22.9 (a)	20.5 (b)	23.0 (a)	20.6 (b)	22.2 (ab)	23.5 (a)
Distance between trusses (cm)		22.6 (a)	21.2 (ab)	21.2 (ab)	20.7 (b)	19.7 (bc)	19.4 (bc)	18.1 (c)
Stem diameter (mm)		10.5 (bc)	10.4 (bc)	10.5 (bc)	11.2 (ab)	11.1 (ab)	11.6 (a)	10.0 (c)
Leaf length (cm)		43 (a)	41 (abc)	42 (ab)	38 (c)	38 (c)	39 (abc)	38 (bc)
Number of leaves ($plant^{-1}$)		23 (a)	21 (ab)	20 (b)	20 (b)	19 (b)	23 (a)	23 (a)
SLA (m^2 g^{-1})		161 (a)	150 (a)	125 (bcd)	129 (bcd)	115 (c)	129 (bcd)	122 (bcd)
LAI (m^2 m^{-2})		3.64 (b)	3.51 (b)	3.51 (b)	3.61 (b)	3.36 (b)	4.47 (a)	4.67 (a)
Truss development rate ($week^{-1}$)		1.18 (ab)	1.26 (ab)	1.06 (b)	1.34 (a)	1.31 (a)	1.34 (a)	1.33 (a)
Number of new fruits on plant ($week^{-1}$)		8.1 (bc)	8.5 (abc)	7.3 (c)	9.6 (a)	8.2 (bc)	9.2 (ab)	9.4 (a)
Fruit growth period (day^{-1})		62.7 (a)	58.6 (ab)	54.5 (bc)	53.4 (bc)	50.4 (c)	49.0 (c)	49.6 (c)

Table 4: The effects of HPS top light and LED inter-light on fruit quality parameters.

Traits	Treatments	1	2	3	4	5	6	7
	Compartment		1		2		3	
	HPS toplight (W m^{-2})	161	161	161	242	242	272	272
	LED inter-light (W m^{-2})	0	60	120	0	60	0	60
SSC (°Brix)		4.67 (e)	4.84 (de)	4.89 (cd)	5.07 (bc)	5.13 (ab)	5.09 (abc)	5.29 (a)
TTA		0.53 (a)	0.52 (a)	0.51 (a)	0.51 (a)	0.55 (a)	0.52 (a)	0.54 (a)
SSC/TTA		8.81	9.31	9.59	9.94	9.33	9.79	9.80
Firmness		0.89 (a)	0.89 (a)	0.89 (a)	0.85 (b)	0.84 (bc)	0.82 (c)	0.82 (c)

Table 5: The effects of HPS top light and LED inter-light on light and energy use efficiency.

Traits	Treatments	1	2	3	4	5	6	7
	Compartment	1			2		3	
	HPS toplight (W m^{-2})	161	161	161	242	242	272	272
	LED inter-light (W m^{-2})	0	60	120	0	60	0	60
Light use efficiency (g FW mol^{-1})		8.96	7.85	6.35	10.34	8.80	8.60	7.44
R^2		0.995	0.992	0.997	0.995	0.996	0.997	0.994
Energy use efficiency (MJ kg^{-1} FW)		65	71	87	55	63	66	75
R^2		0.994	0.991	0.997	0.995	0.995	0.998	0.994