

## Finding the Optimal Growth-Light Spectrum for Greenhouse Crops

S.W. Hogewoning<sup>1</sup>, G Trouwborst<sup>2</sup>, E. Meinen<sup>3</sup> and W. van Ieperen<sup>4</sup>

<sup>1</sup> Plant Lighting, Utrecht, The Netherlands,

<sup>2</sup> Plant Dynamics BV, Wageningen, The Netherlands

<sup>3</sup> Wageningen UR Greenhouse Horticulture, Wageningen, The Netherlands

<sup>4</sup> Horticultural Supply Chains group, Wageningen University, Wageningen, The Netherlands

**Keywords:** artificial sunlight, cucumber, far-red, light emitting diodes (LEDs), photomorphogenesis, supplemental lighting, tomato

### Abstract

Especially in an open crop (e.g., young plants) morphological responses to light quality can affect light interception, crop photosynthesis and growth. Earlier work showed a substantial morphology related biomass increase for young cucumber plants grown under 100% artificial sunlight (ASL) compared with 100% high pressure sodium light (HPS). Here, ASL is used to investigate the effect of HPS and LEDs compared with ASL, when applied supplemental to an ASL background. Tomato plants were grown in a climate room under 17 h ASL (50% of in total  $200 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$ ) supplemented with 50% HPS, light emitting diodes LEDs (red/blue), or ASL. The 100% ASL-grown plants produced 32-45% more dry weight, due to a more efficient light interception. As ASL lamps are not energy-efficient enough for commercial production we tried to simplify the solar spectrum while retaining enhanced crop productivity in greenhouses. Red/blue/far-red LEDs, at a ratio inducing the same phytochrome photostationary state (PSS) as natural sunlight, and sulphur-plasma lamps, emitting a continuous spectrum in the PAR-region, were tested and compared with supplemental red/blue LEDs, HPS and ASL in a greenhouse experiment. Red/blue/far-red LEDs resulted in a visual appearance similar to the ASL-plants, while red/blue LEDs produced the most compact morphology. Red/blue/far-red LEDs enhanced dry weight for cucumber (+21%) and tomato (+15%) compared with HPS. Dry weight and compactness were intermediate for sulphur-plasma. The differences were attributable to effects of leaf orientation and positioning on light interception, and not to photosynthesis per unit leaf area. The PSS appears to be a key-factor to control crop morphology, providing a tool to induce 'sunlight' crop characteristics to enhance productivity.

### INTRODUCTION

The influence of light on the growth and development of plants is dual: light is an energy source for carbon fixation (i.e., photosynthesis) and a signal source to control developmental processes (i.e., photomorphogenesis). The wavelengths most efficient for driving photosynthesis (photosynthetically active radiation; PAR) fall in the range of 400-700 nm. Photomorphogenetic responses are sensitive to both PAR and far-red (700-750 nm) wavelengths, depending on the photoreceptors involved (Whitelam and Halliday, 2007). Although a distinction is often made between 'assimilation light' for biomass production and 'signalling light' for control of morphology and development, signalling light can also affect biomass production: blue light can increase the photosynthetic capacity per area of leaf (Matsuda et al., 2004; Hogewoning et al., 2010b) and light intercepting area is an important determinant of crop photosynthesis (e.g., Poorter and Nagel, 2000), which may act via morphology, leaf orientation and growth direction. Especially in an open canopy where incident light is only partially intercepted (e.g., young plants), signalling responses may have a strong impact on crop productivity.

In a growth chamber experiment a large increase in biomass production was shown for young cucumber plants grown under artificial sunlight (ASL), compared with high pressure sodium lamps (HPS) or white fluorescent tubes (Hogewoning et al., 2010a).

It was concluded that the increased productivity under ASL was due to a more efficient interception of light while measured photosynthesis per leaf area could not explain the differences observed. It is not known if comparable effects occur when HPS and ASL are applied supplemental to a full spectrum daylight background.

Therefore, young tomato plants were grown in a climate chamber with ASL as a full spectrum daylight background and supplemented with HPS or light emitting diodes (LEDs) or ASL. Although the development of ASL has been a step forward for research, ASL does not appear to be competitive in terms of efficiency ( $\mu\text{moles photon output per Joule energy input}$ ). Therefore we also investigated if a simplified solar spectrum could have similar advantageous effects on plant productivity under greenhouse conditions. White fluorescent tubes, HPS lamps, or red and combined red and blue LEDs all have in common that they produce compact plants. This is, at least partially, due to a (near) deficiency of far-red wavelengths, which strongly influence the phytochrome photo-equilibrium (Morgan and Smith, 1979). Therefore it was hypothesized that the phytochrome photo-equilibrium may play a crucial role in the development of plant morphological characteristics advantageous for light interception. On the other hand, sunlight has a continuous spectrum representing the complete wavelength range important to plants while the spectra of common growth-lamps are not continuous. Therefore supplying a continuous spectrum of wavelengths covering the complete 'PAR-range' may also trigger the desired plant responses. These two hypotheses were tested on young cucumber and tomato plants in a greenhouse. The daylight in the greenhouse was supplemented with HPS lamps (commercial reference), ASL (qualitative reference for visual appearance), red/blue LEDs, red/blue/far-red LEDs and sulphur-plasma lamps (continuous, but not sunlight spectrum).

## MATERIALS AND METHODS

### Climate Chamber Experiment

Tomato plants (*Lycopersicon esculentum* 'Red Sky') were sown on peat-based compost and transferred after 15 days to a climate chamber which was divided into three light-tight sub-compartments with similar climate conditions (22/20°C day/night, 17 hour photoperiod, 75% RH). To simulate light conditions in winter,  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  artificial sunlight (ASL; Fig. 1B) was provided in each compartment and supplemented with another  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  from either high pressure sodium lamps (HPS) or mixed red/blue LED light (20% blue (450 nm), 80% red (660 nm); RB-LEDs), or ASL. Artificial sunlight was provided by a modified microwave-driven plasma lamp (Plasma International GmbH, Offenbach am Main, Germany). The water-cooled LED system was supplied by Lemnis Lighting BV (Barneveld, The Netherlands). Per compartment, 12 plants were grown on height adjustable tables to maintain a light intensity of  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$  at canopy top. Plants were rotated regularly to eliminate variation due to heterogeneity in light intensity ( $200 \pm 12 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Leaf temperature was monitored over 24 h on four plants per treatment using a thermocouple at the abaxial leaf surface. Plants were harvested after 21 days light treatment and plant length, number of leaves, total leaf area, truss number, diameter of the fourth internode, leaf mass per area (LMA) of fully expanded leaves, total dry weight (excluding roots) and dry weight of the lateral shoots were determined on eight plants per treatment.

### Greenhouse Experiment

Tomato (*Lycopersicon esculentum*; scion: 'Mecano') and cucumber (*Cucumis sativus* 'Venice') were sown in rockwool under normal cultivation conditions. On 18 October 2011 the young plants were transferred to the concrete floor in the greenhouse compartment. For cucumber this was six days after sowing. The tomato plants were sown earlier, grafted, and pruned to two shoots per plant prior to transfer. Ten plots of  $10 \text{ m}^2$  in a  $480 \text{ m}^2$  greenhouse compartment were separated with plastic sheets (white towards the plants) allowing the entrance of ample daylight on the south side of the plots. Cucumber

(18 plants m<sup>-2</sup>) was placed on one side of each plot and tomato (12 plants m<sup>-2</sup>) on the other. Common commercial cultivation practice was applied for both species. Except for the lighting treatments all conditions were similar in all plots.

Plants were illuminated with five different spectral treatments in duplo (0.00-16.00 h, 75  $\mu\text{mol m}^{-2} \text{s}^{-1}$  supplemental lighting in all plots): (1) Supplemental HPS (Philips Greenpower Plus 1000W, 400V; common practice reference), (2) ASL (as described above; qualitative reference for visual morphological appearance under 100% sunlight), (3) RB LEDs (15% blue/85% red), (4) RB-FR LEDs (15% blue/85% red combined with far-red), (5) sulphur-plasma (Hogewoning et al. 2010a). Figure 1 shows the spectra of all supplemental lighting sources used. The peak wavelength of the red, blue and far-red LEDs was 450, 635 and 733 nm, respectively.

The spectral composition of treatment (4) was comprised so that the phytochrome photostationary state (PSS; Sager et al., 1988) was similar to that of natural daylight. Within plots, plants were rotated regularly to minimize variations due to heterogeneity in light intensity. Because the heterogeneity of the light intensity in treatment 2 was high, no quantitative data are shown for this treatment. In treatment (4), 22% of the photon flux emitted by the far-red LEDs was counted as PAR as absorbed far-red wavelengths can contribute to photosynthesis (Hogewoning et al., 2012). To prevent large temperature effects on plant responses, the LEDs were supplemented with infra-red heaters (medium wave IR heater, Heraeus Noblelight, Hanau, Germany). The power settings of the heaters were based on apex temperature measurements by a type-K thermocouple.

Leaf photosynthesis-light response curves were measured short before harvest on three leaves per plot per species using a Li-6400-40 portable photosynthesis measuring system (Li-cor, Lincoln, NE, USA) according to Trouwborst et al. (2010). The CO<sub>2</sub> concentration was set similar as greenhouse air (500 ppm). Measurements were made on the second leaf of the cucumber plants and on the third leaf of one of the shoots of the tomato plants. The plants were harvested when they started shading each other: 20 days (cucumber) and 15 days (tomato) after start of the lighting treatments. Dry weights of leaves and stem, total leaf area, stem length, petiole length of the second (cucumber) or third (tomato) leaf, stem diameter at the first (cucumber) or third (tomato) internode, and the number of leaves were measured. LMA was determined for the second and third leaf for cucumber and for all leaves for tomato. All measurements were made on the oldest shoot for tomato (N=10 per plot). For cucumber 32 plants per plot were measured in pairs (N=16), except for the number of leaves, and stem length and diameter (N=32 per plot).

The experiment was repeated for cucumber ('Amaranta') in December with less treatments (i.e., HPS, RB LEDs and RB-FR LEDs) and only one, larger, plot per treatment. Fisher's LSD was used to make post-hoc multiple comparisons among spectral treatment means from significant one way ANOVA tests (P<0.05).

## RESULTS AND DISCUSSION

### Climate Chamber Experiment

Compared with supplemental HPS, plant length, total leaf area and total shoot dry weight were significantly higher under ASL and lower under the RB-LEDs (Table 1). The percentage of dry weight allocated to the lateral shoots was lower for the ASL (2.1%) than for the two other treatments (4.0-5.1%). LMA was highest for supplemental ASL. No significant differences were found for stem diameter, and the number of leaves and trusses (Table 1). Visually the plants supplemented with RB-LEDs appeared to be darker green and with ASL lighter green, compared with supplemental HPS. In contrast to ASL, leaves grown under LEDs and, to a lesser extent, also under HPS showed malformations (curling, excessive intervenal growth of leaf tissue) and a downwards directed leaf orientation, whereas the malformations were not visible for the leaves developed under ASL. No significant differences in the average 24 h leaf temperatures were measured. These results clearly show that supplemental ASL enhances productivity of young tomato plants more than supplemental HPS and RB-LEDs, presumably due to a plant

morphology advantageous for light interception (longer stem, larger leaf area, non-curved leaves). Leaf photosynthetic rates were not measured in this climate chamber experiment. Notably, the relative DW allocated to lateral shoots was lowest in the ASL plants (Table 1). This might have been related to the induction of a less active state of phytochrome B by the sunlight spectrum, compared with the (nearly) far-red deficient HPS and RB LEDs spectra, affecting apical dominance and the degree of lateral bud outgrowth suppression (Domagalska and Leyser, 2011). In this climate chamber experiment the light use efficiency of supplemental HPS and RB-LEDs was less than that of sunlight, showing that spectral modifications may improve the effectiveness of growth-light lamps.

### **Greenhouse Experiment**

Despite the extremely sunny weather in October 2011 (34% more sun-hours than average; Dutch meteorological institute KNMI), clearly different plant responses to different supplemental light spectra were found: plants supplemented with ASL and RB-FR LEDs had a similar visual appearance and were most elongated, while plants supplemented with RB-LEDs were most compact (Fig. 1). In both species, total accumulated biomass (DW) was lowest for RB LEDs and HPS, intermediate for sulphur-plasma and highest for RB-FR LEDs (Table 2). The RB-FR LEDs treatment produced 21 and 15% more DW for cucumber and tomato, respectively, than HPS. Differences in leaf DW, total leaf area, leaf number and LMA were insignificant or small. Differences in stem DW followed a similar trend as total DW: RB-FR LEDs produced 50 and 47% more stem DW for cucumber and tomato, respectively, than HPS. Sulphur-plasma also produced substantially more stem DW (+20 and +24%) than HPS. Quantitatively the differences in total plant DW are largely due to the differences in stem DW. Differences in stem length followed a similar trend as stem DW, whereas differences in stem diameter were either small (tomato) or insignificant (cucumber). In cucumber the petiole length followed a similar trend as stem DW and length: +65, +33 and -11% for the supplemental RB-FR LEDs, sulphur-plasma and RB LEDs, respectively, compared with HPS. In tomato no significant differences in petiole length were found. Overall, the light-saturated photosynthetic rate ( $P_{max}$ ) was higher for tomato than for cucumber (Fig. 2). Overall the photosynthesis-light response curves show little differences between treatments in both species. Only the  $P_{max}$  of cucumber leaves grown under red/blue LEDs was slightly lower than  $P_{max}$  in the other treatments. At lower light intensities, which are representative for winter greenhouse conditions, the differences in leaf photosynthetic rate between treatments were negligible. The greenhouse experiment was repeated in December 2011 (cucumber only), when natural daylight was substantially less abundant than during the 1<sup>st</sup> experiment. Plant responses to the different supplemental lighting sources followed similar trends, but the differences were larger (data not shown). For instance, stem length was +70% (+29% before) and -21% (-16% before) for RB-FR LEDs and RB LEDs, respectively, compared with HPS. Also, whereas no significant differences were found for the number of leaves before (Table 2), now supplemental RB-FR LEDs resulted in significantly more leaves per plant (5.7) compared with RB LEDs (5.1) and HPS (5.0).

Therefore it is concluded that the substantial differences in DW with different supplemental growth-light sources are largely related to morphology related differences in light interception, caused by differences in petiole and/or internode length (Table 2) and also to leaf orientation (not shown), and not to differences in leaf photosynthetic rate.

The 2<sup>nd</sup> greenhouse experiment for cucumber in December resulted in a somewhat larger number of leaves for the supplemental RB-FR LEDs treatment. This could be a cultivar effect, and/or due to the larger impact of the supplemental light on plant development, as in December natural daylight is relatively scarce. Also, the total tomato leaf area was largest for ASL in the climate chamber experiment (Table 1), whereas no difference in leaf area was found in the greenhouse experiment (Table 2). The response of leaf area to light-spectrum may be cultivar dependent, or may be related to the relatively large proportion of natural daylight compared with the amount of supplemental light

during October in the greenhouse. Considering the visual appearance of the plants (Fig. 1), the morphological parameters discussed, and the light spectra used, the results strongly suggest that the phytochrome photostationary state (PSS) is a major determinant for plants to develop a ‘sunlight’ morphology. This would also explain the intermediate response with regard to many of the measured parameters for sulphur-plasma light (Table 2; Fig. 1). Far-red wavelengths have a strong impact on the PSS (Sager et al., 1988) and the sulphur-plasma spectrum contains a substantial amount of far-red wavelengths (Fig. 1E), however, less than in natural sunlight, ASL and the RB-FR LEDs. From productivity point of view a supplemental lighting spectrum promoting ‘sunlight characteristics’ would be a way to exploit combined assimilation and signalling properties of light. This would be expected to be especially effective in open crop stands. For other purposes more compact plant characteristics may be desirable (e.g., ornamental plants). The signalling properties of supplemental light will have larger consequences for plant morphology when daylight is relatively scarce.

## ACKNOWLEDGEMENTS

This research is supported by the Dutch Program ‘Kas als Energiebron’ funded by the Ministry of Economic Affairs, Agriculture and Innovation and Productschap Tuinbouw; we thank research coordinators Leo Oprel and Dennis Medema for their support. We are grateful to Hortilux Schröder BV, Lemnis Lighting BV, and Plasma International GmbH for supplying light sources. We acknowledge Jan Snel, Henk Jalink, Andreas Savvides, Evert Janssen, Rob van der Schoor and the Unifarm staff (all Wageningen UR) for supporting the climate room experiment. Regarding the greenhouse experiment we acknowledge Peter de Jong, Jilles Koornneef, Ewald de Koning and other staff of ‘Plantenkwekerij van der Lugt’, Piet Steenbergen (WUR-Greenhouse Horticulture) and Sander Pot (Plant Dynamics BV).

## Literature Cited

- Domagalska, M.A. and Leyser, O. Signal integration in the control of shoot branching. *Nat. Rev. Mol. Cell Biol.* 12:211-221.
- Hogewoning, S.W., Douwstra, P., Trouwborst, G., van Ieperen, W. and Harbinson, J. 2010a. An artificial solar spectrum substantially alters plant development compared with usual climate room irradiance spectra. *J. Exp. Bot.* 61:1267-1276.
- Hogewoning, S.W., Trouwborst, G., Maljaars, H., Poorter, H., van Ieperen, W. and Harbinson, J. 2010b. 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. Bot.* 61:3107-3117.
- Hogewoning, S.W., Wientjes, E., Douwstra, P., Trouwborst, G., van Ieperen, W., Croce, R. and Harbinson, J. 2012. Photosynthetic quantum yield dynamics: from photosystems to leaves. *Plant Cell Advance Online*. doi:10.1105/tpc.112.097972.
- Matsuda, R., Ohashi-Kaneko, K., Fujiwara, K., Goto, E. and Kurata, K. 2004. Photosynthetic characteristics of rice leaves grown under red light with or without supplemental blue light. *Plant Cell Phys.* 45:1870-1874.
- Morgan, D.C. and Smith, H. 1979. Function of phytochrome in the natural environment. 8. A systematic relationship between phytochrome-controlled development and species habitat for plants grown in simulated natural radiation. *Planta* 145:253-258.
- Poorter, H. and Nagel, O. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO<sub>2</sub>, nutrients and water: a quantitative review. *Aust. J. Plant Physiol.* 27:595-607.
- Sager, J.C., Smith, W.O., Edwards, J.L. and Cyr, K.L. 1988. Photosynthetic efficiency and phytochrome photoequilibria determination using spectral data. *Trans. ASAE* 31:1882-1889.
- Trouwborst, G., Oosterkamp, J., Hogewoning, S.W., Harbinson, J. and van Ieperen, W. 2010. The responses of light interception, photosynthesis and fruit yield of cucumber to LED-lighting within the canopy. *Physiol. Plant.* 138:289-300.

Whitelam, G. and Halliday, K. 2007. Light and Plant Development. Oxford, Blackwell Publishing.

## Tables

Table 1. Plant properties of tomato ('Red Sky') grown in a climate chamber under  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  artificial sunlight (ASL) supplemented with  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  provided by HPS lamps, LEDs (20% blue, 80% red), and ASL (i.e.,  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$  ASL).

	Artificial sunlight supplemented with:		
	HPS	LEDs (r/b)	ASL
Stem length (cm)	35.5 <sup>b</sup>	29.4 <sup>c</sup>	39.7 <sup>a</sup>
Stem diameter (mm <sup>2</sup> )	9.2 <sup>ns</sup>	9.5 <sup>ns</sup>	9.5 <sup>ns</sup>
Number of leaves	11.6 <sup>ns</sup>	11.3 <sup>ns</sup>	11.6 <sup>ns</sup>
Number of trusses	2.6 <sup>ns</sup>	2.9 <sup>ns</sup>	2.8 <sup>ns</sup>
Total leaf area (cm <sup>2</sup> )	1193 <sup>b</sup>	990 <sup>c</sup>	1478 <sup>a</sup>
LMA (g m <sup>-2</sup> )	23.3 <sup>c</sup>	25.9 <sup>b</sup>	32.4 <sup>a</sup>
Total dry weight (g)	6.5 <sup>b</sup>	5.9 <sup>c</sup>	8.6 <sup>a</sup>
% DW lateral shoots	4.0 <sup>a</sup>	5.1 <sup>a</sup>	2.1 <sup>b</sup>

Different letters indicate significantly different means ( $P < 0.05$ ;  $N = 8$ ; ns = not significant).

Table 2. Plant properties of cucumber ('Venice') and tomato (scion: cv. Mecano) grown in October 2011 in a greenhouse with  $75 \mu\text{mol m}^{-2} \text{s}^{-1}$  supplemental light (0h:00-16h00) provided by high pressure sodium (HPS) lamps, LEDs (blue/red), LEDs (blue/red/far-red) or sulphur-plasma light (non-solar).

	Cucumber				Tomato			
	HPS	LEDs (r/b)	LEDs (r/b/fr)	Sulphur Plasma	HPS	LEDs (r/b)	LEDs (r/b/fr)	Sulphur Plasma
Stem length (cm)	50.3 <sup>c</sup>	42.3 <sup>d</sup>	64.9 <sup>a</sup>	58.2 <sup>b</sup>	45.7 <sup>c</sup>	44.8 <sup>c</sup>	56.9 <sup>a</sup>	53.0 <sup>b</sup>
Petiole length (cm)	8.6 <sup>c</sup>	7.7 <sup>d</sup>	14.2 <sup>a</sup>	11.5 <sup>b</sup>	9.0 <sup>ns</sup>	8.9 <sup>ns</sup>	8.3 <sup>ns</sup>	9.0 <sup>ns</sup>
Stem diameter (mm)	8.3 <sup>ns</sup>	8.5 <sup>ns</sup>	8.7 <sup>ns</sup>	8.4 <sup>ns</sup>	7.8 <sup>b</sup>	8.2 <sup>a</sup>	8.0 <sup>ab</sup>	7.9 <sup>b</sup>
Number of leaves	6.6 <sup>ns</sup>	6.3 <sup>ns</sup>	6.6 <sup>ns</sup>	6.6 <sup>ns</sup>	7.8 <sup>ns</sup>	7.9 <sup>ns</sup>	7.9 <sup>ns</sup>	7.6 <sup>ns</sup>
Total leaf area (cm <sup>2</sup> )	1565 <sup>ns</sup>	1595 <sup>ns</sup>	1560 <sup>ns</sup>	1508 <sup>ns</sup>	1340 <sup>ab</sup>	1381 <sup>a</sup>	1345 <sup>ab</sup>	1279 <sup>b</sup>
LMA (g m <sup>-2</sup> )	15.3 <sup>ns</sup>	14.9 <sup>ns</sup>	16.1 <sup>ns</sup>	16.1 <sup>ns</sup>	30.7 <sup>ns</sup>	31.7 <sup>ns</sup>	29.9 <sup>ns</sup>	30.1 <sup>ns</sup>
Total dry weight (g)	3.7 <sup>c</sup>	3.6 <sup>c</sup>	4.5 <sup>a</sup>	4.0 <sup>b</sup>	5.2 <sup>b</sup>	5.2 <sup>b</sup>	6.0 <sup>a</sup>	5.4 <sup>b</sup>
Dry weight leaves (g)	2.5 <sup>ns</sup>	2.6 <sup>ns</sup>	2.7 <sup>ns</sup>	2.5 <sup>ns</sup>	3.6 <sup>ab</sup>	3.7 <sup>a</sup>	3.6 <sup>ab</sup>	3.5 <sup>b</sup>
Dry weight stem (g)	1.2 <sup>c</sup>	1.0 <sup>d</sup>	1.8 <sup>a</sup>	1.5 <sup>b</sup>	1.6 <sup>c</sup>	1.5 <sup>c</sup>	2.3 <sup>a</sup>	1.9 <sup>b</sup>

Different letters indicate significantly different means per species ( $P < 0.05$ ;  $N \geq 32$  (cucumber);  $N = 20$  (tomato); ns = not significant).

## Figures

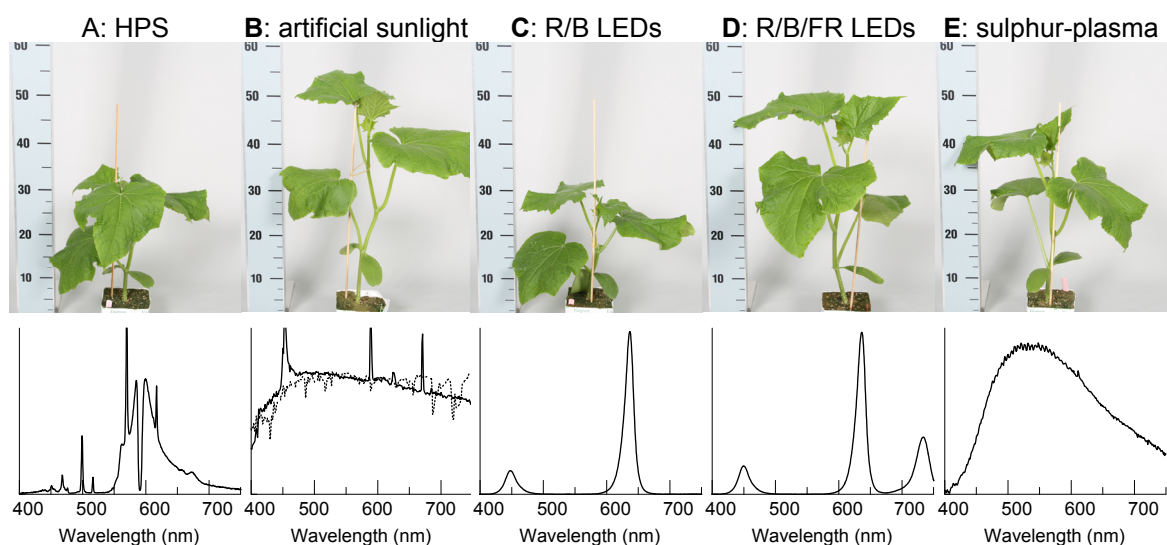


Fig. 1. Above: representative cucumber plants 4 days before harvest grown in the greenhouse under five different supplemental light sources during 18 October-07 November 2011. Below: the corresponding spectra (relative photon flux) of the supplemental light sources in the range 400-750 nm. The dotted line in figure B represents a natural solar spectrum, whereas the solid line indicates the artificial solar spectrum.

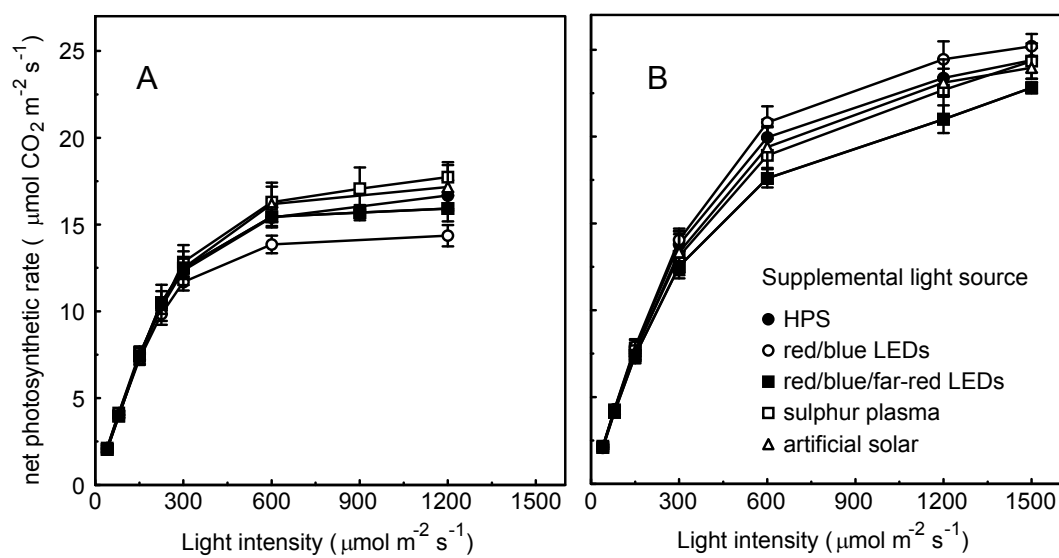


Fig. 2. Leaf photosynthesis-light response curves of cucumber (A) and tomato (B) grown under different supplemental lighting sources in October-November 2011. The legend in B also applies for A. Error bars indicate the s.e.m. (N=6).

