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Sustainable crop production in greenhouses based on crop physiological understanding

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Abstract

A more precise control of the growth conditions has led to a strong increase of crop yield in greenhouses. To further improve crop production, product quality and sustainability we need a profound knowledge of the responses of the plants to environmental conditions as well as crop management by growers (e.g. pruning, plant density).

In young plants, initially rapid leaf formation boosts production due to its role in intercepting light. However, we propose that many full grown crops invest too much assimilates in new leaves.

Responses of plants to the environment are seldom linear and show many interactions. Furthermore, short and long terms responses can be very different due to acclimation and feed-back mechanisms. Therefore, research should not only study plant responses under constant conditions, but also analyse multiple interacting factors in fluctuating conditions.

Controlling the climate should focus more on the microclimate near the plant organs than on the average greenhouse climate. For instance, the temperature of the apical meristem may deviate 4°C from that of the air. Leaf initiation rate depends on temperature of the apical meristem independent of the temperature of the other plant organs and this has a significant impact on the plant phenotype.

LED lamps open opportunities for energy saving while improving growth, yield and product quality, as they allow the instantaneous control of spectrum, intensity and direction of light, and the decoupling of lighting from heating. Effects of LED light on yield can be attributed to effects on leaf photosynthesis, plant morphology which affects the absorption of light, and dry matter partitioning. LED light can also trigger secondary metabolites resulting in increased disease resistance, or increased anti-oxidants such as vitamin C or anthocyanins. A next step in the control of the production process is indoor production without solar light in vertical farms. This step is boosted by developments in LED technology.

Keywords: Light emitting diodes, dynamic photosynthesis, macroclimate, microclimate, leaf area, controlled environment agriculture

INTRODUCTION

In the Netherlands, in about 25 years the annual production per unit greenhouse area (kg m⁻²) increased by 113% in tomato, 90% in sweet pepper, and 35% in cucumber (De Gelder et al., 2012). To a large extent this increase was due to a more precise control of the growth conditions in greenhouses. To further improve crop production, product quality and sustainability we need a profound knowledge of the responses of the plants to environmental conditions as well as crop management by growers (e.g. pruning, plant density). Responses of plants to the environment are seldom linear and show many interactions (Poorter et al., 2013). Interactions of climate factors can be found on many plant processes. For instance the optimum temperature for photosynthesis varies with

growth temperature (acclimation), CO₂ concentration and light intensity (Qian et al., 2012; Yamori et al., 2014). The optimal set-point for air temperature is different whether LEDs or high pressure sodium lamps are used as supplementary light in a greenhouse (Dueck et al., 2012). Furthermore, short and long term responses can be very different due to acclimation and feed-back mechanisms. For instance, light intensity has no effects on the fraction of dry matter partitioned to the fruits in cucumber on the short term (few days; Marcelis, 1993). However, in the long term (weeks) increasing light intensities increase the fraction of assimilates to the fruits due to a stimulation of fruit set (Marcelis, 1993). Therefore, research should not only study plant responses under constant conditions, but also analyse multiple interacting factors in fluctuating conditions.

The introduction of LED lighting in greenhouses opens up many new possibilities for growers to control the production and quality of the harvested products, while saving energy. Besides their use in greenhouses, LEDs also boost vertical farming (indoor crop production without solar light). Optimizing the light intensity should always be done in consideration with all other growth factors. So far, climate control focuses on control of temperature, humidity and CO₂ concentration of the air as measured in one central measuring box in the greenhouse (i.e. macroclimate). However, the climate the plant experiences might differ from this macroclimate. For a more precise control, growers should look at the climate around the plant organs (i.e. microclimate).

Besides controlling all climatic conditions, a grower has to make a number of decisions about crop management, such as plant density and (leaf) pruning. Considering optimization of climate, the leaf area of plants deserves special attention. A high leaf area is essential for intercepting the light. Furthermore, leaf area affects greenhouse climate and energy use via transpiration. On the other hand, in many crops the harvestable products are not leaves, making an excessive investment in leaf formation suboptimal.

In this paper, we will discuss four items which can play an important role in further improving yield and sustainability of crop production in controlled environment agriculture. First, we will discuss the role of leaf area for plant growth and will show that often plants invest too many assimilates in the formation of new leaves. Second, the differences between macroclimate and microclimate and consequences for plant growth will be discussed. Third, we will discuss fluctuations of light intensity in greenhouses and their implications for production, breeding and research. Finally, we will focus on how production, quality and energy use can be affected by LED lighting.

OPTIMAL LEAF AREA FORMATION

In young plants, a rapid leaf area formation is crucial for high plant growth rate. In this growth stage, a relatively low fraction of light is intercepted by the canopy, while crop growth strongly relates to intercepted light. Light interception of a canopy can be described by the law of Lambert–Beer (Monsi and Saeki, 2005):

$$I_{int} = 1 - e^{-kL} \quad \text{Eqn. 1}$$

Where I_{int} is the fraction of light intercepted by the canopy, L is the leaf area index (LAI, m² m⁻²) and k is the extinction coefficient. Typical values for k are in the range of 0.5 to 0.8 and in crop models often a value of 0.7 is used (Marcelis et al., 1998). This equation (Eqn. 1) predicts that when k is 0.7, 88% of the light is intercepted when the leaf area index is 3 m² m⁻². Increasing leaf area index to 4 m² m⁻² would lead to about 6%-point higher fraction of intercepted light. Further increases in LAI result only in small increases in the fraction of intercepted light. Expected increases in gross photosynthesis rate are of similar magnitude. This shows that if LAI is low (e.g. lower than 3 m² m⁻²) a strong gain in gross canopy photosynthesis is possible by increasing leaf area, but at higher LAI (e.g. higher than 4 m² m⁻²) the returns on the investments in additional leaf area are diminished severely. In a tomato experiment three different LAI treatments were tested by picking different numbers of old leaves. Reference, high and maximum LAI resulted in average LAI of 3.3, 3.6 and 4.1 m² m⁻², respectively, and equal yields of 66 kg m⁻² (Heuvelink et al., 2005).

Many crops (in greenhouses as well as in the open field) form a LAI much larger than 4. For instance, in sweet pepper the leaf area index can reach values of 7 or 8 (Dueck et al., 2005). Also, for crops like chrysanthemum (LAI up to 7; Lee et al., 2002), cut-rose (LAI 4-6; Kool and Lenssen, 1997), gerbera (LAI 4-7; De Visser et al., 2014) and strawberry (LAI 3-11; Mochizuki et al., 2013) large leaf area indices have been reported. Besides the already mentioned positive effects of high leaf area index on gross canopy photosynthesis, there might also be downsides of a high leaf area index.

Firstly, young, growing leaves compete for assimilates with other sink organs. Several studies in tomato have shown that removal of young leaves can reduce the construction costs of leaves and promote the growth of other organs like fruits and flowers. Removal of young leaves reduces the total sink strength of the vegetative part of the plant. The fraction of assimilates partitioned into an organ is proportional to the ratio of its sink strength and the sum of sink strengths of all organs (Marcelis, 1996). Therefore, removal of vegetative sinks will lead to a higher fraction of assimilates partitioned into the fruits (Fig. 1). Removal of young leaves while maintaining the total leaf area at a reasonable level (about 3 m² m⁻²) may improve fruit yield in tomato by up to 10% (Heuvelink et al., 2005). At present, many Dutch tomato growers apply removal of young leaves during some periods of the year.

Secondly, a larger leaf area (when this involves a higher leaf mass) might also result in higher rates of maintenance respiration, which means that the relative effects on plant growth are probably smaller than the relative effects of leaf area on canopy photosynthesis (Heuvelink et al., 2005).

Thirdly, a high leaf area index may lead to high transpiration rates and humid microclimate. Dueck et al. (2005) estimated that in a sweet pepper crop removal of 60% of the leaves in August from the lower part of the canopy would reduce annual crop transpiration by 10% (75 litres of water per m²). From the end of August onwards, growers are often facing a too high air humidity in the greenhouse. They can reduce this by heating while the windows are open. However, this comes at a cost of using fossil energy. It was estimated that the removal of 60% of the leaves in sweet pepper could lead to a 5% saving on annual energy consumption (Dueck et al., 2005). A lower leaf area index might also lead to a less humid microclimate inside the canopy, possibly decreasing risks for fungal diseases.

Figure 1. Schematic presentation showing the effect of leaf:truss ratio on assimilate partitioning between leaves and trusses in tomato. At the left a plant with 3 leaves and 1 truss and at the right a plant with 2 leaves and 1 truss. Numbers inside organs represent sink strength of the organs. Percentages represent the fraction of assimilates partitioned to the organ, resulting from these sink strengths.

Considering the high leaf area index realised in many crops, we propose that an increase in yield of horticultural crops where the harvestable products do not consist of leaves, is possible by limiting the formation of leaves once a reasonable leaf area (LAI of about 3 to 4 m² m⁻²) has been reached.

FROM MACROCLIMATE TO MICROCLIMATE

Growers usually control the climate (temperature, air humidity, CO₂ concentration) in their greenhouses based on one measuring box above or at a high location in the canopy. However, there can be both vertical and horizontal variation in the greenhouse (e.g. Bojacá et al., 2009; Kempkes et al., 2000; De Gelder et al., 2012). Furthermore, the climate around plant organs may deviate from that in the measuring box and in particular temperature of the organ may deviate from that of the air.

Qian et al. (2012a; 2015) studied vertical gradients in temperature and air humidity in semi-closed greenhouses where cooled and dehumidified air was blown into the greenhouse from below or above the canopy. The set-points of the climate control were such that it maintained the same temperature and air humidity at the top of the plants in the two treatments. Cooling from below the canopy induced vertical temperature and vapour pressure deficit (VPD) gradients. The vertical temperature and VPD gradients were most pronounced from June to September. At high radiation levels in the afternoon, temperature at the bottom of the canopy was 5°C lower and VPD was 0.7 kPa lower than at the top of the canopy. No substantial vertical temperature and VPD gradients were detected in greenhouses with cooling from above. Despite these large differences in vertical temperature gradients, plant growth and fruit yields were mostly unaffected. Leaf and truss initiation rates did not differ between treatments, since air temperatures at the top of the canopy were comparable. The only observed response of the plants to the vertical temperature gradient was the reduced rate of fruit development in the lower part of the canopy. This resulted in a longer time between anthesis and fruit harvest in the treatment with a vertical temperature gradient, and an increase in the average fruit weight in summer. However, total fruit production over the whole season was not affected.

Measurements from 6 gerbera cut-flower companies showed that during day time the air humidity between leaves was distinctly higher than that in the measuring boxes where the humidity of the air just above the canopy was measured (Van Os et al., 2009). Interestingly, the air humidity near flowers was distinctly lower than at the measuring box. This may have consequences for botrytis development, a fungal disease that can lead to severe financial losses.

Savvides et al. (2013) showed that in tomato and cucumber the shoot apical meristem substantially deviated from air temperature even in moderate environments. This deviation varied between -2.6 and 3.8 °C in tomato and between -4.1 and 3.0 °C in cucumber. The observed differences in temperature of the meristem between the two species studied were due to differences in apical bud structure and transpiration. This deviation was a function of other environmental factors, such as radiation, air humidity and wind speed. Subsequently, Savvides et al. (2016) showed that leaf initiation rate was determined by the apical bud temperature independent of the temperature of other plant organs or the air. These findings trigger the question if such spatial temperature differences also influence leaf expansion and plant phenotype. In a 28 day study, Savvides et al. (2017) maintained temperature differences between temperature of the apical bud and the rest of plant ranging from -7 to +8 °C using a custom-made bud temperature control system. Leaf expansion did not only depend on leaf temperature but also on the difference between bud and leaf temperature. Differences between bud temperature and plant temperature considerably influenced vertical leaf area distribution over the shoot: increasing bud temperature beyond that of the plant resulted in more and smaller leaves, while decreasing bud temperature below that of the plant resulted in less and larger leaves (Fig. 2). The trade-off between leaf number and leaf area resulted in phenotypic alterations that cannot be predicted, for example, by crop models, when assuming plant temperature to be uniform.

These results on climatic differences in a greenhouse and differences between plant organs are important when designing greenhouses and heating and cooling systems as well as the set-points for climate control.

Figure 2. Two-dimensional illustration of the phenotypes of cucumber plants when subjected to (a) increased whole plant temperature and (b) increased apical bud temperature. At a given temperature of the plant, increasing temperature of the apical bud resulted in taller plants with more phytomers like in plants under increasing whole plant temperature; however, much less biomass and leaf area were distributed per phytomer (left to right) in comparison to plants under increasing whole plant temperature. (reprinted from Savvides et al., 2017).

FLUCTUATING LIGHT INTENSITIES: IMPLICATIONS FOR PRODUCTION, BREEDING AND RESEARCH

Light intensities display large fluctuations in greenhouses. An example is shown in Fig. 3, which was recorded at several layers in a rose canopy in a research greenhouse in Wageningen, the Netherlands. In this example, several peaks exceeding $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ are visible around noon. Similar fluctuations were recorded on a daily basis over a period of 6 months (data not shown), indicating that fluctuating light is by no means exceptional in greenhouses. This is despite an absence of wind, which causes most, and with the highest frequency fluctuations in the field. Light fluctuations in the greenhouse are caused by clouds, as well as by shade and reflection of greenhouse construction, which moves during the day as a consequence of the diurnal movement of the sun. On a clear day, light fluctuations are therefore stronger than on a cloudy day (Li et al., 2016). Fluctuating light intensities have several major implications for researchers, breeders and growers: they reduce light use efficiency, they can flag up phenotypes not visible in constant light, and they might change the acclimation of leaf photosynthesis to light.

In the steady state, i.e. when all environmental factors are stable, net photosynthesis rate (A_n ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) is limited by the rate of electron transport, the capacities for electron transport, RuBP regeneration, carboxylation rate, the rate of sucrose phosphate utilisation, as well as stomatal and mesophyll conductances (g_s and g_m ; $\text{mol m}^{-2} \text{s}^{-1}$) that determine the rate of CO_2 diffusion towards the chloroplast (Farquhar et al., 1980; Farquhar and Sharkey, 1982; von Caemmerer, 2000; Flexas et al., 2008; Simkin et al., 2015). In fluctuating light, limitations are added to A_n that stem from the regulation of processes reacting to changes in light intensity, because the activity of these processes is dependent on light intensity, and because their activation or deactivation does not change instantaneously, transient A_n after a switch in light intensity is often lower than steady-state A_n . Processes such as ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco) activation, the activation of enzymes regulating RuBP regeneration in the Calvin cycle, stomatal movement, and non-photochemical quenching react to changes in light intensity with a time constant that causes A_n to be lower than it is in constant light intensities (Percy et al., 1996; Way and Percy, 2012; Kaiser et al., 2015; 2016; Kromdijk et al., 2016). This also implies that models which have been parameterised using only steady-state data (e.g. Farquhar et al., 1980) will overestimate A_n in fluctuating light intensities, as they assume instantaneous responses of A_n to changes in irradiance (Percy et al., 1997; Naumburg and Ellsworth, 2002; Timm et al., 2004). Rapid changes in light intensity will also change leaf temperature and vapour pressure deficit between the leaf and the air surrounding it ($\text{VPD}_{\text{leaf-air}}$; Schymanski et al., 2013), and these climatic factors by themselves also affect A_n and g_s . These interactions are further complicated by the fact that the capacity of A_n to react to a sudden increase in light intensity is pathway-dependent. This means that A_n in a leaf that was exposed to shade before the increase in light intensity will react more quickly to light intensity increases than a dark-adapted leaf, because the processes potentially slowing down the increase in A_n in high light are more strongly activated in shade than they are in darkness. Also, A_n in a leaf that was exposed to darkness for only 1 minute will respond more quickly to light intensity increases than a leaf that was darkened for 10 minutes.

The speed with which A_n responds to a change in light intensity is further modulated by the environmental factors CO_2 partial pressure, temperature and $\text{VPD}_{\text{leaf-air}}$. An increase in CO_2 partial pressure increases A_n in fluctuating light intensities, through a combination of reduced diffusional limitation, faster activation of Rubisco, and reduced photorespiration, which reduces the post-illumination CO_2 burst (Leakey et al., 2002; Tomimatsu and Tang, 2016; Kaiser et al., 2017). An increase in leaf temperature until approx. 30°C tends to increase the rate of increase of A_n after a stepwise increase in light intensity, but further increases in temperature are detrimental (Kaiser et al., 2015). Increases in $\text{VPD}_{\text{leaf-air}}$ have been found to slow down the rate of increase of A_n after switches from low to high light

intensity; this effect is caused by an initially low g_s , which slows down CO_2 diffusion towards the chloroplast and could directly slow down the rate of Rubisco activation (Kaiser et al., 2017). Interactions of A_n in fluctuating light intensities with other environmental factors are especially relevant to plant growth in greenhouses, as the environmental factors listed above can be controlled closely, allowing growers and scientists to adjust the environment in such a way that light intensity fluctuations are used optimally.

Large-scale phenotyping, for example using chlorophyll fluorescence to show differences between genotypes for a given treatment (e.g. van Rooijen et al., 2015), is becoming an ever more important and powerful tool in modern plant breeding and research. Typically, just as in experiments using leaf gas exchange, all conditions are kept stable. However, because the screening often aims at selecting genotypes that would perform well in the field (i.e. in fluctuating light conditions), during screenings where only constant light conditions are used, genotypes might be overlooked that would perform best in the field: using a climate-chamber based imaging system equipped with dynamic light control, Cruz et al. (2016) showed that phenotypes of several mutants of *Arabidopsis thaliana* only showed differences compared to the wildtype in constant light, while others only differed from the wildtype in fluctuating light. This approach is a powerful demonstration of large genotypic variability that may affect growth and fitness in the field and would be ignored under standard, steady-state conditions.

Apart from the short-term reactions described above, fluctuations in light intensity can lead to acclimations. In fluctuating light intensities, leaves typically upregulate photosynthetic capacity (light- or CO_2 -saturated A_n), compared to leaves grown at constant light intensity, while both treatments have the same average light intensity (Retkute et al., 2015; Violet-Chabrand et al., 2017). The effects of light fluctuations on acclimation are larger the longer duration of the periods at high light intensity (Walters, 2005; Alter et al., 2012). While the acclimation of A_n to light fluctuations is still a relatively understudied topic that deserves more attention (Violet-Chabrand et al., 2017), the implication is that leaf photosynthetic capacity might be underestimated in plants grown under (naturally) fluctuating light. This would be overlooked when growing plants in constant light intensities such as in climate chambers.

Figure 3. Diel time course of photosynthetically active radiation outside the glasshouse, inside the glasshouse just above a cut-rose canopy and in the canopy (at 33% height from bottom to top of canopy) on a sunny day (26/5/2016). Radiation inside the greenhouse was measured every second by a point sensor (Li-190R), while outside radiation was estimated measured by a solarimeter (Kipp & Zonen).

LED LIGHTING

The fact that growers want to increase the level of control of the production process is reflected by the increased use of lighting in greenhouses in the Netherlands. In the 1980's many rose growers invested in assimilation lighting. Later, many other crops followed. In about the year 2000 the first tomato growers started using assimilation lighting. Still, the use of assimilation lighting is increasing. During the last 20 years the electricity used for assimilation lighting in the Dutch greenhouse horticultural sector increased by about 15% per year (data based on statistical information from (van der Knijff et al., 2006; van der Velden and Smit, 2013). So far, almost all the lighting is provided by high pressure sodium (HPS) lamps. However, in recent years a number of growers invested in LED lighting and this number is expected to increase rapidly.

LED lighting opens up many new opportunities for growers. The main differences of LEDs compared to high pressure sodium lamps can be summarised as follows: (1) the energy use of the latest LEDs is less than that of HPS lamps, (2) the spectrum can be modified, (3) they generate less heat radiation, (4) they can be positioned close to plants and in between the canopy, and (5) can be rapidly switched on/off. The main disadvantage is the high investment costs. The energy use of HPS lamps is usually claimed to be about 1.8 μmol per Joule electricity; Nelson and Bugbee (2014) reported measured efficiency of HPS lamps of 1.7 and Wallace and Both (2016) measured 1.6 μmol per Joule electricity. LEDs come in a wide range of energy efficiencies. The latest LEDs seem to have an efficiency of about 2.7 μmol per Joule electricity (Kierkels, 2017) and some companies already claim efficiency up to 3 $\mu\text{mol}/\text{J}$.

In the Netherlands, a modern tomato grower with HPS lighting uses typically 3100 MJ m^{-2} fossil energy per year, of which 80% consists of electricity for lighting (2480 MJ m^{-2}) (Vermeulen, 2012). The remaining 20% (620 MJ m^{-2}) is mainly used for heating and humidity control. Furthermore, 530 MJ m^{-2} of the lighting energy (i.e. 530 out of 2480 MJ m^{-2}) also contributes to fulfilling the energy demand for heating and humidity control; hence a total of 1150 MJ m^{-2} is used for heating and humidity control. Several studies (e.g. De Gelder et al., 2012) have shown that Next Generation Cultivation (also called "The New Way of Growing") can reduce the energy demand for heating and humidity control by 30-40%. The main components of this concept are an intensive use of energy screens to conserve heat, controlled inlet and distribution of outside air to regulate air humidity, and flexible temperature set-points based on energy losses and plant demand. Hence, about 7% energy of the total fossil fuel consumption (35% of 620 MJ m^{-2} saves 215 MJ m^{-2}) could be saved in this way. The main bottleneck for energy saving remains the energy use for lighting. LEDs can play an important role here due to their efficient conversion of electricity to light. Furthermore, by making use of the special features (spectrum, timing, positioning, separation of heat and light) of LEDs we can increase the light use efficiency of plants, which adds to the total energy efficiency. In 2015, we started a five-year research programme, called LED it be, that aims to realise a substantial (more than 50%) saving on energy in tomato production by the smart use of LEDs. The research in this project focuses on improving the light use efficiency (production per unit of light from the lamps) of the tomato crop by 30%; hence allowing a further improvement of energy saving on electricity by 30%. Eight PhD students and 3 postdocs have been appointed at five Dutch universities and they cooperate with 10 private companies: LTO Glaskracht, Philips, Bayer Crop Science, Rijk Zwaan, Bejo Seeds, Hortimax, Van der Lugt, Westlandse Plantenkwekerij, B-Mex and WUR Greenhouse Horticulture. We estimated that compared to HPS lighting, at least 30% improvement of light use efficiency should be possible by three main routes: Improved light absorption by adapted canopy architecture and positioning of LEDs can save 15% energy; 10% percent energy saving can be realised by improved photosynthesis; and 5% by improved assimilate partitioning. Furthermore, lighting might be used to enhance disease resistance of the crop and decrease transpiration at moments that transpiration leads to energy costs.

Improved light absorption can be realised by improving the positioning of the lamps. For instance, often about 7% of the photosynthetically active radiation coming from above is reflected by a canopy (Marcelis et al., 1998) and 5-10% of the light vanishes unused in the floor (Heuvelink et al., 2005). Several authors concluded that positioning the lamps in between the canopy can improve production compared to lamps above the canopy, due to the better light absorption and better vertical light distribution (e.g. Hovi-Pekkanen and Tahvonen, 2008), although in some experiments no substantial yield improvement was found by interlighting compared to lamps above the canopy (Trouwborst et al., 2010; Dueck et al., 2012). More attempts at optimization of interlighting are needed to fully exploit its potential benefits. Furthermore, Sarlikioti et al. (2011) estimated that adapted plant morphology can improve crop photosynthesis by 10% due to better light distribution. Diffusing greenhouse covers can increase crop growth by 5-10% (Li et al., 2014) indicating that improving the distribution of light absorption in a canopy is of great benefit. It is a challenge to find the optimal crop architecture and positioning of the lamps in order to improve the light absorption and photosynthesis of the crop.

An improvement of light use efficiency by at least 10% due to improved photosynthesis seems feasible, considering that the quantum yield of photosynthesis is spectrally dependent (McCree, 1972; Hogewoning et al., 2012). Paradiso et al. (2011) estimated a 12% higher canopy photosynthesis under red LED compared to HPS lamps, when applied as supplementary light in a greenhouse. Furthermore, if photosynthesis would be continuously monitored, a further improvement of photosynthesis seems likely possible by lowering the light intensities at moments that the photosynthetic efficiency is low.

Finally, we anticipate that light use efficiency can be improved by at least 5% by improved partitioning of assimilates to the fruits of tomato. So far, little research has been performed on spectral effects of light on partitioning to the fruits.

Besides effects on crop growth and development LED lighting might affect the content of secondary metabolites in plants. For instance, plant defence mechanisms (increased salicylic acid and pathogen related enzymes) against fungal diseases might be triggered by light (Vänninen et al., 2012). LED lighting may also affect the susceptibility to herbivorous insects and interestingly it may affect the predators of these insects as well (Cortés et al., 2016). In addition, the quality of the harvested products might be affected. For instance, illuminating developing tomato fruits with LEDs resulted in a substantial increase of vitamin C content of the fruits (Ntagkas et al., 2016).

In this paper, we have focused on production in greenhouses. However, the rapid technological improvements in LED lighting opens up opportunities for vertical farming, where plants are grown indoors without solar light. Research on effects of LED Lighting on plant physiology, growth and production of plants in greenhouses and vertical farms (climate chambers without solar light) will result in further optimization of both production systems.

CONCLUSIONS

- In plant research, more attention is needed on the interaction between different growth conditions and plant processes, as well as on fluctuations in climatic conditions. Estimating yield in greenhouses or open field, based on research under steady state conditions in climate controlled rooms, might lead to overestimations.
- LED lighting opens up many possibilities to control photosynthesis, morphology, development and growth of plants as well as product quality for production of plants in greenhouses or vertical farms.
- We propose that many fully grown crops invest too many assimilates in new leaves. Removal of young leaves can substantially improve crop yield.
- Controlling the climate should focus on the microclimate near the plant organs rather than on the average greenhouse climate.

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