Effect of far-red light on improving yields of tomatoes produced in vertical farms

Advances in plant factories

Ji, Yongran; Butturini, Michele

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Chapter 14

Effect of far-red light on improving yields of tomatoes produced in vertical farms

Yongran Ji and Michele Butturini, Wageningen University & Research, The Netherlands

1 Introduction

Tomato (*Solanum lycopersicum* L.) is one of the major crops cultivated globally and one of the most important vegetable crops in the world. Global tomato production has increased substantially from ~35 million tonnes in the 1970s to ~186 million tonnes in 2020 (FAOSTAT, 2023). With a significant production area being temperate zones, tomatoes are also produced in tropical and subtropical climate zones around the globe. China (65 million tonnes), India (21 million tonnes), Turkey (13 million tonnes), the United States (12 million tonnes), and Egypt (7 million tonnes) are the primary producers of tomatoes ranked by total production (Table 1). Tomato varieties differ in their shapes and sizes. They can be categorised as follows: classic round, plum and baby plum, beefsteak, cherry and cocktail, vine or truss, and regional varieties and landraces. Tomatoes are produced for fresh consumption or food processing and can be grown in the open field or a protected environment such as greenhouses.

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Table 1 Major tomato-producing countries (areas) ranked by total production in 2020

Area	Total Production (million tonnes)	Total harvested area (thousand ha)
China (Mainland)	64.8	1107. 5
India	20.6	812.0
Turkey	13.2	181.9
United States of America	12.2	110.4
Egypt	6.7	170.9
Italy	6.2	99.8
Iran (Islamic Republic of)	5.8	129.1
Spain	4.3	55.5
Mexico	4.1	84.9
Brazil	3.8	52.0

Source: FAOSTAT.

Although tomatoes are produced mainly in open fields, the production of tomatoes in a protected environment has expanded rapidly in recent decades. Compared to conditions in an open field, growth conditions in protected horticulture ensure more stable crop production and enable year-round production. Optimising growth conditions and breeding for cultivars suitable for production in a protected environment, the average yield of tomatoes has continuously increased over the years. In the Netherlands, for example, where tomatoes are mainly produced in greenhouses, the average yield is 60–70 kg m^{-2} and is substantially higher than the global average (Heuvelink, 2018).

1.1 Yield determination in tomato

Tomato yield, which is evaluated by the fresh mass of the fruits, can be divided into multiple components (Fig. 1). Fruit fresh mass is determined by the fruit water content and fruit dry mass. The dry mass of the fruit is the result of the accumulation of sugars transported into the fruit from the leaves. Fruit dry mass is divided into total plant dry mass and dry mass partitioning to fruits. Total plant dry mass is determined by leaf net photosynthesis and leaf area index, where leaf area index is further defined by leaf number per plant and leaf area per leaf. Dry mass partitioning in fruits is determined by relative fruit sink strength and total fruit number, further defined by truss appearance rate and fruit number per truss. Each component positively correlates with the plant's fresh fruit mass (yield). For example, yield increase due to higher fruit water content results in fruits with more water, while yield increases due to higher plant dry mass lead to fruits with more fruit tissues.

Yield can also be increased by a larger number of fruits per plant due to an increased truss appearance rate or increased fruit number per truss. However, characteristics can cancel each other out. For example, a fresh fruit mass may

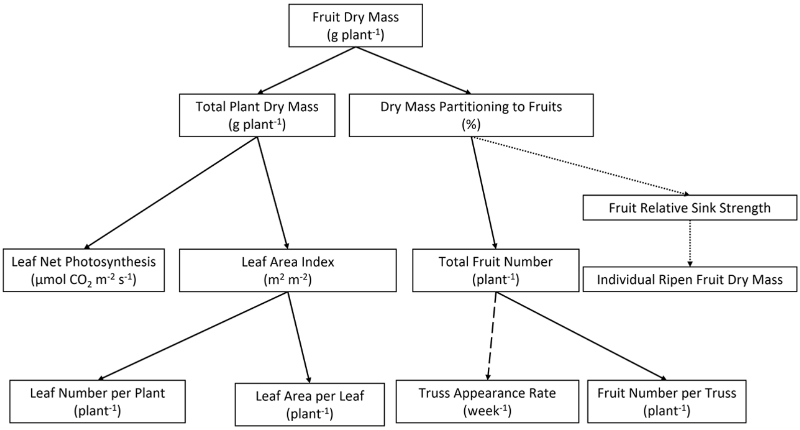

Figure 1 Yield component analysis used in this experiment (adapted from Ji et al. (2019)). Dashed lines indicate that the component was not directly measured but was indirectly estimated.

remain unaffected if the increase in the fruit dry mass is similar to the decrease in fruit water content.

With a detailed understanding of components affecting yield, it is possible to quantify changes in each component between treatments, such as environmental factors and genetic differences, and evaluate their influences on the final yield. For example, Higashide and Heuvelink (2009) analysed morphological and physiological changes in breeding of nine varieties to explain that the yield improvement of these cultivars through 50 years of breeding, finding improvements were mainly due to higher leaf photosynthesis and lower light extinction coefficient.

1.2 Supplemental lighting in tomato greenhouse production

Improved control of climate parameters, such as temperature, humidity, and CO_2, has substantially improved recent yields of tomatoes in greenhouses. In addition to this improvement, supplementary lighting is a common practice for tomato production in greenhouse areas with limited solar radiation during winter. Traditionally, gas discharge-type lamps, such as high-pressure sodium (HPS) lamps, were used to provide supplementary lighting. There has been a recent increase in the popularity of using light-emitting diodes (LEDs) as an alternative light source. LED lighting features several advantages, such as a higher efficacy in converting electricity to photon energy, extended longevity, and higher flexibility in the placement on top or within the plant canopy. Katzin et al. (2021) showed that replacing HPS lamps (efficacy = 1.8 µmol J^{-1}) with LEDs (efficacy = 3 µmol J^{-1}) can reduce annual total energy consumption by up to 27% even when heating is required.

LED lighting fixtures offer the additional benefit of controlling the light spectrum, enabling greenhouse growers to use fully customised light recipes for supplementary lighting. Furthermore, LEDs can provide photons within 400–700 nm (traditionally known as photosynthetically active radiation, PAR) and can also supply photos within the far-red range (FR, 700–800 nm). Unlike photons from the PAR range, FR photons have little activity in driving photosynthesis independently. FR acts synergistically with photons in the PAR range to improve the overall quantum yield (Zhen et al., 2021). Adding FR alters the ratio between red (R) and FR photons.

A cassette of photoreceptors called phytochromes senses this change. Phytochromes exist as two isoforms:

- The Pr form (red-absorbing, biologically inactive); and
- The Pfr form (far-red-absorbing, biologically active).

The light spectrum thereby determines the equilibrium between Pr and Pfr. The Pfr isoform then translocates into the nucleus and mediates a series of photomorphogenic responses collectively known as the shade avoidance syndrome (SAS). Typical SAS responses such as stem elongation, leaf hyponasty, reduced branching, and accelerated flowering have been intensively studied in model species such as *Arabidopsis thaliana* (Casal, 2012). FR may also be supplied as additional lighting in the greenhouse to promote crop production. Several authors reported improved crop growth in leafy crops like lettuce when grown with additional FR (Li and Kubota, 2009; Zou et al., 2019; Zhen and Bugbee, 2020), and such increase was further studied in vertical farming conditions at different planting densities (Jin et al., 2020).

Yield improvement was also reported in tomato crops grown with additional FR (Hao et al., 2016; Kalaitzoglou et al., 2019; Zou et al., 2019). Hao et al. (2016) observed increased yield when adding 8, 16, and 24 μmol m^{-2} s^{-1} of FR to a background HPS lighting of 165 μmol m^{-2} s^{-1}. Kalaitzoglou et al. (2019) experimented with LED lighting and reported increased tomato yield when FR was added during and at the end of the photoperiod. Zou et al. (2019) reported a similar positive effect of FR provided as overhead lighting while the background LED lighting was provided as intra-canopy lighting.

In this chapter, we summarise our recent research published in Ji et al. (2019, 2020, 2021) on the physiological and molecular mechanisms in which FR increased tomato yield. Subsequently, we discuss the possible application of this knowledge to vertical farming and some key aspects for the future improvement of tomatoes grown in vertical farms.

2 Far-red light affects dry mass production and shoot: root ratio in young tomato plants

We conducted an experiment, as has been published by Ji et al. (2021), to explore the genotypic variation in tomatoes' growth responses to FR. Thirty-three different tomato genotypes with significant differences in morphology, growth patterns, and growth rates were grown at 0, 25, or 100 μmol m^{-2} s^{-1} of FR added to a red + white LED light background at μmol m^{-2} s^{-1}. Ten days after sowing, uniform seedlings were transplanted to the experimental climate chamber and were grown for 21 days, after which the plants were destructively harvested, and traits including the dry mass of leaves, stems, roots, as well as plant height, were measured. The total dry mass of the plant responded strongly and positively within one-third of the tested genotypes, while the other genotypes showed moderate or no responses. For almost all genotypes, a significant increase in stem dry mass and plant height was observed FR increased.

Interestingly, more photosynthetic assimilates were partitioned to sustain the growth of stems and/or leaves, as demonstrated by the increased shoot: root ratio. This increase by FR in shoot: root ratio is in line with previous studies in tomatoes (Cao et al., 2018; Kasperbauer, 1987; Lee et al., 2016). Despite all the genotypes showing a higher shoot: root ratio under FR, the underlying processes leading to this increase differed across different genotypes. For some genotypes, this increase correlated with an increase in the dry mass of leaves, stems, and roots with a stronger increase in the shoot dry mass. For some others, however, leaves, and root dry mass both decreased, with a stronger relative decrease of root dry mass. Adding FR suppresses the activity of phytochromes in mediating growth and development. This suggests that phytochromes and hormonal regulation may play a crucial role in mediating the shoot: root ratio responses.

3 Far-red light increases tomato yield by increasing dry mass partitioning to fruits

We conducted an experiment, as has been published by Ji et al. (2019), where tomato plants (*S. lycopersicum* L. cv Moneymaker) were transplanted into the experimental greenhouse three weeks after sowing. With a background of a red + blue (RB) LED lighting at 150 μmol m^{-2} s^{-1}, two FR treatments ~30 and 50 μmol m^{-2} s^{-1} were included, providing light conditions with phytochrome photostationary state (PSS) of 0.84 and 0.80, respectively, compared to the PSS of 0.88 in the RB treatment. We measured the growth and development of tomato plants grown under different light conditions according to a modified yield component analysis scheme (Fig. 1). Comparisons were made between

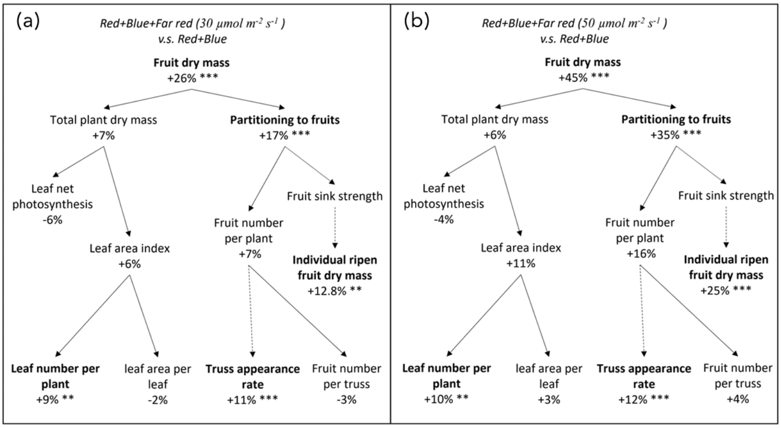

Figure 2 Effects of (a) 30 μmol m^{-2} s^{-1} and (b) 50 μmol m^{-2} s^{-1} of additional far red in a red and blue background light on the growth components. Dashed lines indicate that the parameter was based on estimation. Asterisks denote significant effects of additional FR as tested by linear regression (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Fruit sink strength was not measured. (Adapted from Ji et al. (2019)).

each of the FR and RB reference treatments for each component and tested for their statistical differences.

The yield component analysis showed that, when compared to plants grown without FR, fruit dry mass was significantly increased by 26% at 30 μmol m^{-2} s^{-1} of FR and was further increased by 45% at 50 μmol m^{-2} s^{-1} of FR (Fig. 2). In both cases, total plant dry mass was 6–7% higher, but their differences were not statistically significant. FR significantly increased dry mass partitioning to fruits by 17% and 35% in the two FR treatments. It is clear from the yield component analysis that the increase in fruit dry mass was mainly the result of an increased fraction of dry mass partitioned to the fruits, accompanied by a slight increase in total plant dry mass. An improved light distribution may explain the increase in total plant dry mass in the canopy as FR increased the internode length and led to a more open canopy architecture which, in turn, allowed a deeper radiation penetration into the canopy (Zou et al., 2019). Sarlikioti et al. (2011) used model simulation and showed that an increase in internode length indeed increased the canopy photosynthesis rate by up to 6–8% due to increased canopy light absorption in the upper part of the tomato plant canopy.

Interestingly, FR also increases in the individual fruit dry mass of ripened fruits, which may indicate that the sink strength of individual fruits was increased. Sink strength is the intrinsic capacity of an organ to attract photosynthetic assimilates from the assimilate source (Marcelis, 1996). In tomatoes, the sink strength of the fruit is quantified as the growth rate of tomato fruits under non-limiting assimilate supply, which is also often termed the potential growth rate of the fruit. At a given time during growth, the fraction of dry mass partitioned to the fruits is calculated as total fruit sink strength (sum of individual fruit sink strength existing on a plant at a given time divided by the total plant sink strength, i.e. the sum of fruit sink strength and vegetative sink strength).

Similar to the previous experiment, we set up a new experiment (as published by Ji et al. (2020)) to determine the effect of FR on fruit sink strength and to evaluate whether this effect can explain the previously observed effect in dry mass partitioning. To determine the potential growth rate of tomato fruits, we measured the height and diameter of the fruits on the second, third, and fourth truss of plants pruned to one or two fruits per truss. This measurement was taken non-destructively twice a week. Here, we assumed that the fruits with only one fruit per truss grew without any source limitation. We calculated the size of tomato fruits based on the routine non-destructive measurement of their height and diameter every 2–3 days. Fruit fresh mass was converted to fruit dry mass according to Li et al. (2015) and Maaike Wubs et al. (2012) and then fitted with a non-linear mixed model as a function of fruit age by a Gompertz function. The derivative of this function gives the fruit growth rate as a function of fruit age (days after anthesis, DAA).

We compared the fruit growth on plants with one and two per truss, and there was no significant difference even when the fruit load was doubled hence confirming that fruit growth at one fruit per truss was indeed a potential growth. Additional FR significantly promoted potential fruit growth and led to a higher growth rate throughout the fruit growth period. It reached the maximum growth rate at an earlier fruit age (Fig. 3). A higher potential fruit growth rate under additional FR means increased individual fruit sink strength. This result strongly indicated that the increased fruit sink strength may explain the increased dry mass partitioning under additional FR. To quantify this effect, we needed a growth model to simulate the growth of tomato plants in the above-mentioned experimental conditions.

We then used a growth model to simulate a whole tomato plant's daily dry mass production using data of daily average CO_2 partial pressure during the photoperiod, total daily PAR integral, and the leaf area index (Haverkort et al., 2015). The calculated daily dry mass production was then simulated to be partitioned into the fruits and accumulated throughout the experimental season. The simulated fruit dry mass fraction increased from 33% to 40% for the simulation scenarios with five fruits per truss and increased from 40% to 47% for no pruning. These simulated results agreed very well with the measured dry mass partitioning. Considering that only the individual fruit sink strength was altered during the simulation, it can be concluded that the higher fruit sink strength was the major factor explaining the higher dry mass partitioning to fruits.

To summarise, in the two experiments presented here, we combined experimental research and modelling to demonstrate that additional FR increased dry mass partitioning to fruit by increasing individual fruit sink

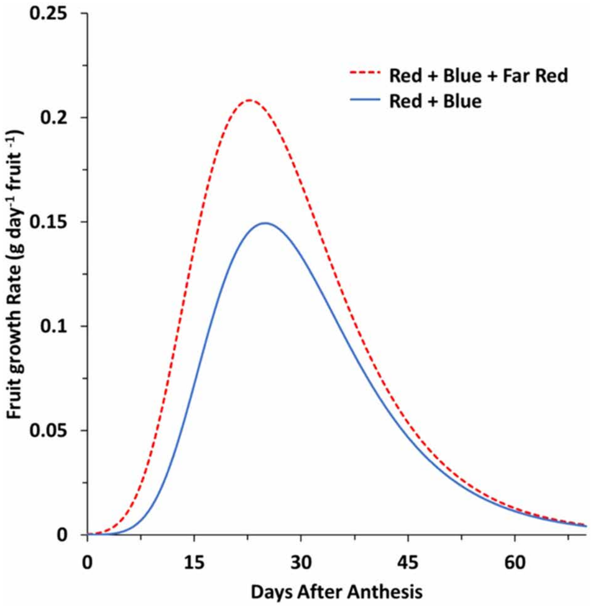

Figure 3 Potential fruit growth rate of tomato (*Solanum lycopersicum*) plants grown with or without additional far red (Ji et al., 2020).

strength. This increase, combined with a slight increase in total plant dry mass, possibly due to a better light distribution within the canopy, led to a higher yield of tomatoes.

4 Physiological and molecular regulation of dry mass partitioning as affected by far-red

Sugar is the building block for plant growth and development. Sugar metabolism in the sink organs is closely linked with the sink strength of these organs (Osorio et al., 2014). We monitored the changes in four major sugars in tomato fruits: starch, fructose, glucose, and sucrose. Tomato fruits typically accumulate starch until around 15–20 days after anthesis before switching to hexose accumulation (Ruan et al., 1997). We observed that starch concentration increased in the fruits until 20 days after the anthesis and decreased to almost zero at ripening.

Additional FR substantially increased the fruits' starch, fructose, and glucose concentrations. Sucrose concentration was not significantly affected by FR. However, considering that a higher concentration of starch, fructose, and glucose was observed, it was reasoned that FR elevated sugar metabolism. Sucrose is the form of sugar being translocated between organs, but FR did not significantly affect its concentration. Considering the elevated sugar metabolism and the higher individual fruit dry mass under FR, it is reasonable to argue that an FR-elevated import rate of sucrose is required to maintain sucrose concentration in the fruit while ensuring a higher fruit growth rate.

In order to further investigate the molecular regulation of sugar metabolism as affected by FR, we studied the key genes involved in sugar transportation and metabolism at different stages of fruit growth. Matching the dynamics of starch concentration during fruit growth, we observed an increased expression of starch synthesis genes during the early days of fruit development, while starch catabolism genes were upregulated after 30 days after anthesis. The upregulation genes encoding sucrose synthase explain the higher fructose and glucose concentration. Invertase genes from *LIN* gene family were also upregulated to further enhance fruit sugar metabolism. Interestingly, the expression of *INVINH1*, which encodes the inhibitor of the invertase Lin5, was also upregulated. The expression of invertase inhibitor caps cell-wall invertase activities to regulate fruit development (Jin et al., 2009). We reason that FR-induced higher sucrose transportation into the fruit to sustain the enhanced sugar metabolism, which supported the upregulation of sugar transporter genes, especially at the flowering stage.

Several key genes involved in sugar transportation and metabolism were previously reported to be regulated by FR or FR-regulatory networks. For example, knocking down phytochromes in the fruit significantly upregulated the expression of cell-wall invertase genes *LIN5* and *LIN6* (Ernesto Bianchetti et al., 2018). Also, Chen et al. (2016) reported that expressions of genes encoding sucrose transporters SWEET11 and SWEET12 were regulated by HY5, a transcription factor directly regulated by FR (van Gelderen et al., 2018).

To summarise, additional FR increased the expression of key genes responsible for fruit sugar transportation and metabolism. Such an increase contributed to a substantial increase in fruit sink strength which quantitatively explained the increase of dry mass partitioning to fruit under additional FR.

5 Current status of tomato production in vertical farming

As one of the most important vegetable crops grown globally, tomatoes are primarily produced in open fields or greenhouses. Greenhouse production typically uses the indeterminant type of tomato growing on the high-wire system to ensure a production period of 9–11 months. Recent years have seen increased interest in using completely enclosed systems (no solar radiation) with total environmental control and artificial lighting to grow crops traditionally grown in open fields or greenhouses. Such facilities, often termed vertical farms or plant factories, are theoretically capable of growing any conventionally farmed crops, and their applications are dictated mainly by the profitability of the products. Currently, the most popular crops for vertical farming are mostly leafy vegetables such as lettuce, basil, and microgreens (van Delden et al., 2021). These crops typically take up little vertical space and can be grown in stacked layers and hence can vastly increase the crop yield per ground area.

Tomatoes are not commonly grown on vertical farms. Having said that, several trials and attempts by researchers and commercial companies have been made to grow tomatoes using vertical farming. For example, the horticultural lighting company Signify (the Netherlands) initiated a long-term study to grow high-wire tomatoes in their GrowWise research centre in 2019 (Mooren, 2021). Certhon (the Netherlands), another Dutch tech company active in the greenhouse and vertical farming business, conducted a 5-year experiment with over 25 cultivation rounds to demonstrate the possibilities of growing cherry tomatoes in vertical farms with a high grade of automation (Breure, 2022). Vertical farming company Infarm (Germany) recently teamed up with Wageningen University and Research (the Netherlands) to sponsor three research projects focusing on the improvement of the production of tomatoes in vertical farms (WUR announces collaboration on crop research with Infarm—WUR, 2022). Similarly, the Foundation for Food & Agricultural Research (United States)'s Precision Indoor Plants consortium awarded a US$2 million grant to the collaboration between the University of Florida (United States), the University of California Riverside (United States), Wageningen University, and Research and Aerofarms (United States) to enhance traits in tomato to make it suitable for indoor production.

Despite active trials and research projects, few companies worldwide have attempted commercial indoor tomato production (PIP Consortium Promotes Indoor Tomato Farming– Foundation for Food & Agriculture Research, 2022). In 2020, Madar Farms (United Arab Emirates) announced the development of a large-scale vertical farm in the desert city of Abu Dhabi (World’s first commercial-scale indoor tomato farm to open in Abu Dhabi – Caterer Middle East, 2020). PlantLab (the Netherlands), a Dutch scale-up company, also announced commercial production of tomatoes (Dutch scale-up PlantLab launches first production site in USA, 2020). 80 Acres Farms (United States) has established indoor tomato production facilities in Ohio (Coolidge, 2020). To our best knowledge, a commercially viable production and business model for vertically farmed tomatoes is yet to be demonstrated.

6 Ideotype of vertically farmed tomato

A niche market for vertically farmed tomatoes exists where some customers will prefer premium products at a higher price. The future of tomato production in vertical farms will require a dedicated selection of varieties suitable for the distinct growth condition provided by vertical farms, which differs substantially from the growth conditions in a greenhouse or an open field. However, almost all tomato cultivars currently available on the market are selected and bred in conventional growth conditions, which means that a good performance in these conditions does not guarantee the same performance in vertical farms. The unique nature of vertical farms, such as LED lighting and increased automation, requires new or different traits from existing breeding strategies. This section will discuss some critical traits of an ideotype of a vertically farmed tomato variety.

Several aspects of crop architecture can be optimised for vertical farming. The leaf architecture and branching of the stems should be optimised to allow light penetration throughout the entire vertical profile of the canopy to ensure a uniform light distribution to maximise canopy photosynthesis among all leaf ranks. Similar to varieties grown in greenhouses, breeding for higher harvest index and light interception are also important. Space is expensive and limited in vertical farms; hence good candidate crops for vertical farming maximises space use efficiency. This means that compactness is a key trait for the breeding of dwarf tomatoes to be grown in a stacked layer vertical farming system.

It also remains relevant for high-wire tomatoes to have shorter internodes to allow more trusses to grow within the vertical space limit. This trait may also help reduce labour costs for crop maintenance. It is worth noticing that a shorter internode length may restrict canopy photosynthesis and hence limit dry mass production and limit yield (Sarlikioti et al., 2011). Also, applying FR may lead to a longer internode and a faster increase in plant height and leaf number (Ji et al., 2019). This may lead to more frequent crop maintenance in activities such as crop rotation and pruning and, as a consequence, increase operational costs in high-wire tomatoes.

Other improvements can be achieved in crop physiology, especially in tomatoes' response to light because a significant proportion of the already high energy demand of vertical farming is attributed to lighting. Hence, vertically farmed tomatoes should be selected for their high light use efficiency and capacity to maintain efficiency during a long photoperiod and high photon flux density. Velez-Ramirez et al. (2014) e.g. demonstrated that a single locus conferred tolerance against continuous lighting in tomatoes and showed the potential to overcome the negative responses under continuous lighting. This should be accompanied by adapting varieties to grow in artificial lighting provided by LEDs.

Since it is not affected by the outdoor climate, a vertical farm allows for non-stop operation, and a short growth cycle will allow more production rounds. For this reason, the quick establishment of leaf area during the early stages of vegetative growth, rapid transition from vegetative to the generative stage, and earlier flowering and fruiting are desired (van Delden et al., 2021). Cultivars bred for conventional production often need to consider resistance against biotic and abiotic stress. Often, an improved resistance to pests and pathogens, or an improved tolerance to extreme climate conditions such as drought, heat, or cold, will lead to a trade-off in yield (Lazzarin et al., 2021; Malhotra et al., 2022). For vertical farms, however, the high degree of climate control and improved hygiene standard makes pests and pathogens or suboptimal climates rare. For this reason, breeding for vertically farmed tomatoes can favour selecting for better yield without the limitation of having to be robust for resistance-related traits.

Growers of conventionally produced tomatoes rely heavily on a consistent supply of high quantities at a competitive yield-to-cost ratio to remain profitable. While a high yield remains relevant for vertically farmed tomatoes, it is more important to focus on increasing the consistency and efficiency of supply. The target market for vertically farmed tomatoes may also differ from those produced conventionally. Consumers may pay a premium price for fruit with higher sugar content, vitamin content, and more intense flavour. In addition, vertically farmed tomatoes may also target specific niche markets and customers that require unique colours, shapes, or flavours.

Compared to tomato production in the open field and greenhouses, vertical farming enables a higher degree of automation using sensors to monitor plant growth and robotic machines for crop handling and harvest. Vertically farmed tomato plants should have an architecture that facilitates and benefits from automation. Such traits may include a longer truss and pedicel for easier fruit detection by sensors and cameras. Better fruit shape and texture will allow easy handling by harvesting robots while reduced axillary shoot growth will avoid pruning. Ideally, fruits should be sufficiently distant from the leaves while the flowering and ripening process should be synchronised in the vertical farms to allow maximum efficiency of automated detection and harvesting of fruits.

Knowledge of flowering and fruit development has been well studied in tomatoes (Seymour et al., 2013) and can allow targeted genotyping for ripening-related traits. Advances in understanding the control of branching and fruit truss architecture have provided exciting possibilities to manipulate crop architecture for vertical farming (Kwon et al., 2020).

7 Conclusion and future trends

In this chapter, we have summarised the mechanisms behind increased tomato yield resulting from the application of additional FR in vertical farms, as demonstrated in studies by Ji et al. (2019, 2020). Adding FR during growth substantially increased individual fruit sink strength, allowing fruits to attract more sugar from the pool of photosynthetic assimilates. This increase leads to a higher dry mass partitioning to fruits and consequently increases tomato yield. This study was conducted in the greenhouse and was demonstrated by a climate chamber experiment with artificial LED lighting only (Ji et al., 2020), showing that the yield improvement of FR is also applicable to vertically farmed tomatoes. The high investment and operation costs largely limit crop choice in vertical farming. Nevertheless, it is often argued that fruiting crops such as tomatoes are a logical future step to attempt to scale up vertical farming.

Although the genetics and physiology of tomatoes have been intensively studied for decades, the successful production of vertically farmed tomatoes still requires the dedicated breeding of cultivars suitable for indoor production. Such targeted breeding needs to be conducted in vertical farms and should not be limited to currently existing breeding populations. Revisiting old and wild genotypes and heirloom genotypes for traits lost in the selection for conventional production, as assisted by modern breeding concepts such as *de novo* domestication, will allow for accurate and rapid manipulation of target traits. Breeding may be accelerated even further with speed breeding and genome editing. Further understanding of plant physiology and photobiology and their interaction with vertical farming production environments will support breeding and help establish efficient growing strategies for tomatoes in vertical farming. With optimised engineering and advanced artificial intelligence, coupled with plant sensors and automation, the production of tomatoes and other fruit crops in vertical farms will pose exciting commercial and scientific potential as a significant part of the modern food supply chain.

8 Where to look for further information

Plant's responses to FR has been extensively studied in the past years and several comprehensive reviews have been published on this topic. For example, the review of "Shade Avoidance" (see Casal, 2012 in reference list) provided a complete overview of the mode-of-action of the shade avoidance responses. Further, Demotes-Mainard et al. (2016) summarized the FR responses of plants and their application in horticulture (https://doi.org/10.1016/j.envexpbot.2015.05.010). For a good understanding of tomato and its production, the book "Tomatoes" is recommended (see Heuvelink, 2018 in reference list).

Several universities and research centers are active in the research of FR and its application in indoor crop production. For example, Wageningen University & Research in the Netherlands, China Academy of Agricultural Science in China, Utah State University, Ohio State University, Michigan State University in the United States. Several active research projects are focused on the indoor production of crops such as tomato. For example, the Sky-High project founded by the Dutch Research Council (NWO) and the indoor tomato project founded by the Foundation for Food & Agriculture Research (FFAR).

Also, several important international conferences are of great interest in the field. For example, the International Workshop on Vertical Farming (VertiFarm, held annually), the International Symposium on New Technologies for Greenhouse (GreenSys, held bi-annually), the International Symposium on

Light in Horticulture (LightSym, held every four years) and the International Horticultural Cognress (IHC, held every four years).

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