



# Photoinhibition in Horticultural Crops: An Overview of the Effect of Light Quality and Signaling in the Underlying Photoprotection Mechanisms

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## ABSTRACT

Acclimation to the privileged lighting environment is an important step for the survival of newly developed horticultural plants such as transplants, tissue culture-generated plants, and mature plants when a change occurs in light intensity during the growth period or even during one full day. Capturing excess light energy without an antecedent to acclimation imposes photooxidative cellular damage and photoinhibition in plants. Since carbon utilization may not keep pace with reductive energy production, it renders electron acceptors in the electron transfer chain oversaturated. However, plants are usually equipped with photoprotective mechanisms to attenuate the detrimental effects of excess light energy on the photosynthesis apparatus. In this review, we discussed how different controlled environment horticulture (CEH) systems are embedded with immense opportunities for improving yield and quality. Current understandings of the direct and indirect functional roles of light spectra are discussed in the context of photoinhibition, photoprotection, and their regulatory mechanisms.

## Introduction

### *Light-related challenges in horticulture*

Acclimation to a light-saturated environment is one of the main factors influencing the successful performance of horticultural plant materials in fields or protected cultivations. The provision of a proper lighting environment in controlled

environment horticulture (CEH) systems is a challenging issue. This challenge is sometimes addressed by the application of supplemental lighting via artificial lights. Even sometimes, artificial lights are the sole source of light energy for photosynthesis and biomass production (Lastochkina et al., 2022). Artificial light is regarded as a merit of technology for producers

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since it enables them to increase the daily light integral (DLI) (Gent, 2014). A traditional approach to methods of initiating flowering in short-day plants has been to break nighttime using artificial lights. This approach is still used by greenhouse owners to meet the market demand at appropriate times, while also expanding topics for research on plant physiology (Alden, 2021). However, horticultural plants face high light energy input in different growing environments with a wide range of occurrences from post-production in tissue culture vessels to greenhouses, fields, and orchards. Excess light capture by plants, together with inadequate acclimation, usually results in photooxidative cellular damage through a so-called photoinhibition process (Li et al., 2018). Photoinhibition is defined as the damage to the D1 protein of PSII, which is highly light-sensitive (Li et al., 2018). Damage to the D1 protein threatens the functionality of PSII and thus the quantum yield efficiency of electron transfer through ETC (Demarsy et al., 2018).

The occurrence of photoinhibition is highly plausible in different horticultural plant species and diverse types of growing environments. Therefore, the growers adopt different approaches to prevent photoinhibition (Van Iersel et al., 2016; He et al., 2019; Shomali et al., 2021). The problem of photoinhibition in horticultural plants has attracted significant attention and encouraged scientists to think of strategies to reduce its negative impact on horticultural plants or to unravel the protective mechanisms involved in the prevention of photoinhibition occurrence. In several cases, the importance of considering the photoinhibition problem in horticultural plants is of vital importance for achieving successful productions in horticultural enterprises.

Light intensity can be regarded as photosynthetic photon flux densities (PPFD). It is the main factor in inducing photoinhibition. However, photoinhibition is not always the direct effect of light intensity. Different environmental factors may affect the occurrence and progression of photoinhibition (Takahashi Murata, 2008). Exposure to environmental stresses like cold, salinity, heat, and oxidative stresses are inevitable in the world of plants (Aliniaiefard et al., 2020; Shomali Aliniaiefard, 2020). Environmental stresses do not directly cause photodamage but exacerbate photoinhibition by preventing the repair of PSII, primarily because the stressors downregulate the carbon fixation process, where the reductive energy generated by light reactions is supposed to be utilized. This is followed by consequences such as the accumulation of

reductive energy in ETC, thereby further generating reactive oxygen species. Usually, ROSs prevent the regeneration of the D1 protein which is the main protein in the PSII apparatus. When the extent of D1 degradation surpasses its regeneration, photoinhibition takes place. In such circumstances, the increase in light intensity can amplify the adverse effects of stressors on photoinhibition. As an example, in a study on cucumber, the adverse effects of cold stress were reportedly more prominent on the photosynthetic functionality when plants were exposed to high light intensities (Ashrestaghi et al., 2021). In such a circumstance, light intensities that are inductive for photosynthesis in normal temperatures can disturb the normal photosynthetic functionality and impose photoinhibition.

On the contrary, nitrogen deficiency reportedly diminished the maximum quantum yield efficiency ( $F_v/F_m$ ) of chrysanthemums under low light intensity but had no diminishing effect on plants under high light intensity (Esmaeili et al., 2022). This suggests that not all types of stressors affect the photoinhibition processes.

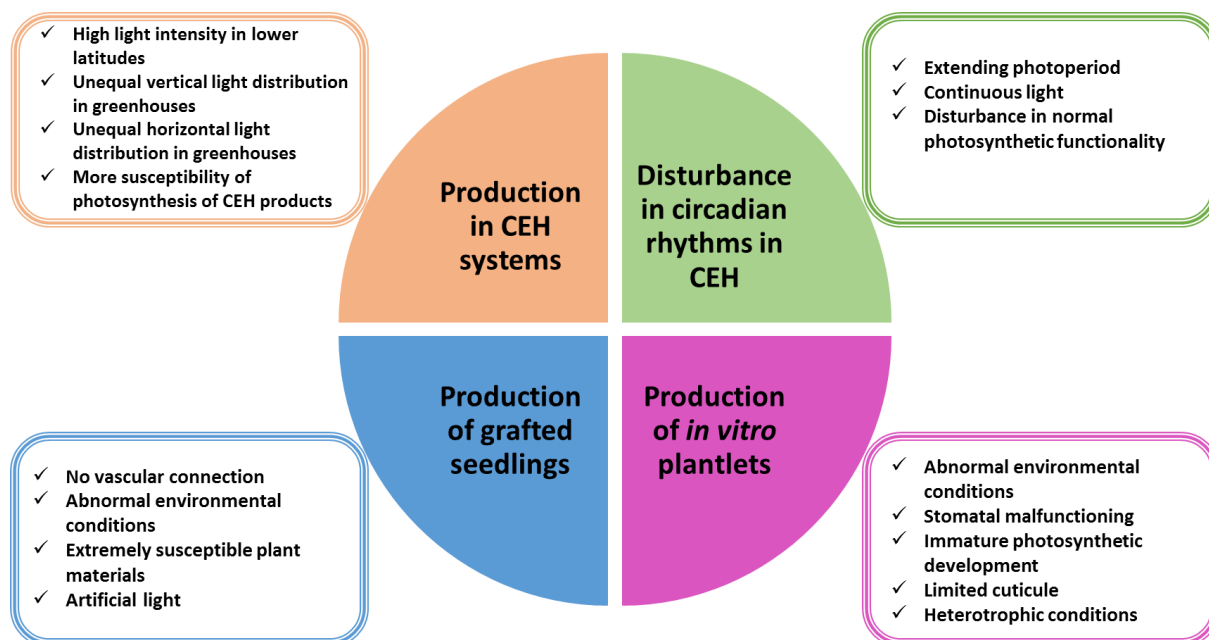
Despite that the occurrence of photoinhibition in fields and orchards depends on the type of horticultural plant species and extreme environmental conditions, some specific or mostly specific settings and practices have been developed to enable the production of horticultural plants in circumstances such as controlled-environment horticultural systems, causation of disturbance in circadian rhythms in horticultural crop production, grafted seedling productions, and *in vitro* propagation of horticultural plants that increase the likelihood of photoinhibition (Fig. 1).

### ***Production in controlled environment horticultural (CEH) systems***

Growth, development, yield, and post-harvest quality of greenhouse crops are directly or indirectly affected by environmental cues, especially on the light level of the CEH systems during the growth of plants (Aliniaiefard and van Meeteren, 2018; Bayat et al., 2018; Min et al., 2021). The importance of light for the greenhouse production of crops is reflected by the design and the structure of greenhouses. As an environmental factor, it is a major determinant of managing crop performance inside greenhouses. In countries located in high latitudes, especially those in northern Europe, supplementary lighting is applied to compensate for sunlight limitations, especially in seasons with short day lengths. In other places, however, having 30° to 45° latitudes,

exposure to high light intensities during the season with long day lengths can negatively influence greenhouse crop production. Greenhouses in those locations are usually

equipped with shading screens to limit the amount of light intensity on crops (Castilla, 2013; Aliniaiefard and van Meeteren, 2018; Javadi Asayesh et al., 2021).



**Fig. 1.** Specific or mostly specific settings and practices for the production of horticultural plants that increase the possibility of the occurrence of photoinhibition. The related causes of photoinhibition are indicated in square boxes.

Greenhouse production is challenged by unequal distribution of light in both vertical and horizontal profiles. For instance, a Chinese solar greenhouse was used in northern China for the production of horticultural crops. This type of greenhouse was characterized by unbalanced structures with an arched front roof that faced the south and a thick wall on the north side. Although production in normal types of greenhouses is challenged with light intensity distribution in a vertical profile, especially when crops have vertical growth patterns, as in cucumber, tomato, and bell pepper, for example, such unbalanced structures in Chinese solar greenhouses have had problems in unequal distribution of light in a horizontal profile of the greenhouse (Tao et al., 2016).

The proper light intensity for the growth of plants in controlled environments (vertical farms, growth chambers, etc.) has been a matter of research during the past decades. Low light intensities in CEH systems not only cause plant deformities such as the occurrence of shade

avoidance response but also limit the yield and production in such systems. Photosynthesis of plants in the CEH systems is usually more susceptible to high light intensities than plants grown on farms. Therefore, increasing light intensity in CEH systems on the one hand, and the occurrence of photoinhibition, on the other, have reportedly increased the cost of production (Min et al., 2021; Moosavi-Nezhad et al., 2022).

Photoinhibition in the production of main greenhouse crops (such as tomatoes, roses, lettuce, chrysanthemum, etc.) reportedly occurred when plants were exposed to high light intensities (Lu et al., 2017; Bayat et al., 2018; Esmaili et al., 2020; Esmaili et al., 2021; Ghorbanzadeh et al., 2021; Hosseinzadeh et al., 2021) or grown under monochromatic red light in controlled environments (Bayat et al., 2018). Furthermore, the effect of desiccation stress on photosynthesis was exacerbated by exposing plants to monochromatic red light depicted by reduced  $F_v/F_m$  of plants (Seif et al., 2021). In another study on roses, it was demonstrated that

plants grown under a full spectrum of light were less affected by photoinhibition, resulting from high levels of light stress, compared to plants grown under monochromatic red and blue light (Bayat et al., 2018). This has been reported in diverse types of horticultural plant species, including cucumber (Hogewoning et al., 2010),

chrysanthemum (Esmaili et al., 2021), roses (Bayat et al., 2018), basil (Hosseini et al., 2019), marigold (Aliniaiefard and van Meeteren, 2018), carnation (Aalifar et al., 2020a,b) and many others. However, the far-red spectrum turned out to have ameliorative effects on photosynthesis (Table 1).

**Table 1.** The role of the far-red light spectrum in the regulation of photosynthesis

| Light spectra  | PPFD   | species                             | Main findings  | reference               |
|--|--|-------------------------------------|--|-------------------------|
| Far-red<br><br>Total                                   | 30-50 $\mu\text{mol m}^{-2} \text{s}^{-1}$<br><br>150 $\mu\text{mol m}^{-2} \text{s}^{-1}$                             | Tomato,<br>Money maker              | Additional far-red increases tomato fruit production mainly by increasing dry mass partitioning to fruits, rather than improving photosynthesis or increasing total biomass.   | (Ji et al., 2019)       |
| Far-red  | 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$   | Macroalgae<br><i>Ulva prolifera</i> | Far-red light can enhance cyclic electron flow around PSI and induce the expression of light harvesting complex stress related gene (LHCSR0 to trigger non-photochemical quenching Fv/Fm and quantum yield of PSII decreased in far-red treatment compared to white light                        | (Zheng et al., 2019)    |
| Blue:<br>Green:<br>Red:<br>Far-red                     | 12.1:42.9:40.6:4.2   | Lettuce                             | The increase in $\Phi\text{PSII}$ by far-red was associated with an increase in net photosynthesis. The stimulatory effect of far-red light increased asymptotically with increasing amounts of far-red.   | (Zhen van Iersel, 2017) |
| Far-red  | 126 $\mu\text{mol m}^{-2} \text{s}^{-1}$<br>(high light)<br><br>15 $\mu\text{mol m}^{-2} \text{s}^{-1}$<br>(low light) | <i>A. thaliana</i><br>'Col-0'       | The CO <sub>2</sub> assimilation rates upon the transition from high light to low light were significantly greater with far-red than without far-red. The enhancement of photosynthesis by far-red was small under the steady-state conditions and in the high light phases of fluctuating light | (Kono et al., 2020)     |
| Far-red<br><br>Total                                   | 49 $\mu\text{mol m}^{-2} \text{s}^{-1}$<br><br>245 $\mu\text{mol m}^{-2} \text{s}^{-1}$                                | hybrid of<br>tomato 'T-34'          | Additional far-red light in the lighting spectrum (red:26, green: 81, red: 93, far-red:49) increased the total dry weight of tomato leaves by 26%, with a lower content of chlorophyll in the leaves.  | (Dorokhov et al., 2021) |
| Red:Far-red=10<br>High<br>Red:Far-red                  | Plants acclimated to saturating irradiance with high and normal red:far-red ratios                                     | Cucumber                            | Net photosynthesis of the high red:far-red leaves was still greater than that of the normal red:far-red leaves at the same intercellular CO <sub>2</sub> concentration (Ci).   | (Shibuya et al., 2010)  |
| Red:Far-red=1.4<br>Normal<br>red: far-red<br><br>Total | 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$   |                                     |  |                         |

Abbreviations: FR: far-red; R: red; B: Blue; G: green; NPQ: non-photochemical quenching; CEF: cyclic electron flow

### ***Disturbance in circadian rhythms in horticultural crop production***

By introducing lighting technology in CEH production systems, plants are exposed to an artificial lighting environment that makes partial or full changes to the growing light environment. For instance, supplementary lighting is applied in greenhouses to extend the photoperiod or to increase the light intensity, especially during periods of light scarcity. More importantly, with the widespread horticultural crop production in vertical farms (or plant factories), light-emitting diodes (LEDs) are a source of light-energy provision for crop production. This facilitates manipulating the lighting environment to improve the yield, quality, and morphology of plants. Sometimes this type of manipulation of the lighting environment involves the extension of the lighting period to 24h at most. In this way, there would be a disruption in the circadian clocks of the plants. Circadian clocks are endogenous timekeepers that autonomously regulate biological systems throughout the day-night cycle (Hsu Harmer, 2014; Yari Kamrani et al., 2022). As an example, the use of supplementary lighting for the production of some horticultural crops such as rose, lettuce, and pepper can be extended to 24 h without a dark period (continuous lighting). The purpose of the extension of the lighting period is to increase growth and yield by extending the photosynthesis duration to 24 h in a non-stop manner (Velez-Ramirez et al., 2011). For instance, the total biomass in roses can be enhanced by 18% when the duration of lighting is increased to 24 h. By continuous lighting, it is possible to increase the number of flowering shoots by 12% and fresh weight per shoot by 5% (Mortensen Gislerød, 1999). In addition to the direct effects of continuous lightening on photosynthesis and growth, pathogenic disorders can be eliminated. For instance, when plants were exposed to continuous light, the occurrence of powdery mildew was restricted (Suthaparan et al., 2010). In contrast, decreasing the lighting cycle to 16 h increased the powdery mildew infection in miniature roses (Mortensen, 2014). Despite these advantages, it has been reported that cultivating plants under disturbed photoperiodic rhythms can result in physiological disorders and cause photoinhibition in plants (Velez-Ramirez et al., 2011). This would result in the development of mottled leaf chlorosis and necrotic spots in tomatoes grown under continuous light, which would be detrimental for susceptible tomato cultivars (Velez-Ramirez et al., 2011). Similarly, in lettuce, although continuous light improved growth and yield, it induced

disturbances in electron transport and photoinhibition (Khoramtabrizi et al., 2018).

### ***Direct evidence of the involvement of light spectra in photoprotection***

Light is one of the most important factors that contribute to the activation of signals that lead to plant fitness in the environment. For instance, the response of plants to blue light via phytochromins is considered an intelligent behavior that evolved through evolution and contributed to plant fitness (Gagliano et al., 2016; Shomali et al., 2022). Direct evidence of the involvement of light spectra in photoprotection has been documented. Different research revealed that different light acclimation regimes affect the ability of plants to cope with photoinhibition. Cultivating *Arabidopsis thaliana* in RL led to lower resistance of the photosynthesis apparatus to UV-A and UV-B, compared to plants grown under white light (WL) (Khudyakova et al., 2017). Although RL pre-illumination boosted plant resilience to UV stress, long-term (0-3h) irradiation of RL resulted in accelerated degradation of photosynthetic pigments and reduced the photochemical activity of photosynthesis in spinach (Kreslavskii et al., 2012). Another study on rose plants demonstrated a lower performance index per absorbed photon (PIABS) in plants grown under RL, compared to plants under WL (Bayat et al., 2018). Furthermore, cucumber plants grown under a monochromatic red spectrum displayed a lower apparent quantum yield of photosynthesis ( $\alpha$ ) which denotes photoinhibition. Plants grown under monochromatic red light also depicted lower flavonoid index (Palma et al., 2021) denoting that the red spectrum suppresses one of the important protective mechanisms in stress response by red spectra (Shomali, 2022). It was also revealed that monochromatic blue and green lights do not interfere with normal photosynthesis while monochromatic red light downregulates photosynthesis. Moreover, under the same light levels, the green spectrum showed low light acclimation because of an altered canopy architecture (Palma et al., 2021). An interesting study in retrograde signaling in rice under blue and red light depicted that red light induces retrograde signaling and causes photobleaching when provided in high intensities, whereas high-intensity blue light induces higher photosynthetic pigments and upregulated the expression of PSBS protein (Duan et al., 2020).

A study on sunflowers revealed that under both moderate and high intensity of white light, the green spectrum was more efficient in driving

photosynthesis compared to the red spectrum. It was claimed that the green spectrum alters the leaf structure and makes it more efficient in absorbing photosynthetically-active radiation, thereby driving carbon fixation efficiently, since it enables a tuned Rubisco/chlorophyll ratio (Terashima et al., 2009).

### ***Indirect evidence of the involvement of light spectra in photoprotection***

Short-term pre-illumination of RL ameliorated the photoinhibition caused by UV stress in WT plants, whereas the degree of UV stress damage in *hy3* mutants (long hypocotyl mutants) was not affected by RL-pre-illumination, thereby suggesting a role for phyB in RL-triggered UV stress response (Kreslavski et al., 2013; Kreslavski et al., 2016). In addition, the ameliorative effects of RL on UV stress damage, removed by FRL, is another evidence for the involvement of phytochromes in the resistance of photosynthesis apparatuses to UV light stress (Kreslavski, et al., 2013). In the same context, the protective role of phytochrome A and B versus UV stress has been demonstrated. Under UV stress, single and double mutants of phyA and phyB of *Arabidopsis thaliana* showed a significantly lower resistance staged by PSII, compared to wild-type (WT) plants (Khudyakova et al., 2017).

The role of photoreceptors in photosynthesis acclimation under UV-B or high light stress has been reported indirectly when studying the response of plants to different light spectra or, directly, through assessing the role of phytochromes, cryptochromes mutants, or overexpressed lines. Photoreceptors contribute to several mechanisms that lead to the adaption of photosynthesis apparatus to oxidative stresses, including antioxidant activities, PSII repair, non-photochemical quenching (NPQ), chloroplast avoidance, and synthesis of sunscreen compounds (Demarsy et al., 2018).

Several reports showed that an increase in the ratio of the Pfr/Ptotal or the ratio of the content of a specific phytochrome, such as PhyB, to the overall pool of all phytochromes can enhance plant resilience against certain stress factors (Thiele et al., 1999; Boccalandro et al., 2009; Kreslavski, Lyubimov, et al., 2013; Kreslavski, Shirshikova, et al., 2013). In this regard, a sufficiently high Pfr/Pr ratio is usually achieved by a high level of red light to far-red (R/FR), which has been highlighted as a possible strategy for reducing the detrimental effects of oxidative stress (Kreslavski et al., 2018). High R/FR improves plant tolerance to UV stress by lowering the degradation rates of chlorophyll a and

chlorophyll b, while reducing the suppression of lipid peroxidation, despite the adverse effects of UV-B exposure. In addition, an increase in the synthesis of anthocyanins is another possible strategy whereby plants respond to UV stress. In particular, this is adapted by plants that grow in high R/FR light regimes (Joshi et al., 1991; Boccalandro et al., 2009). Red light and UV-B light synergistically improved plant antioxidant capacity in cucumbers (Palma et al., 2021).

It was also reported that short-term pre-illumination of RL protects the photosynthesis apparatus against UV stress by lowering the magnitude of decrease in the photochemical activity of PSII, decreasing the H<sub>2</sub>O<sub>2</sub> content, and increasing UV absorbing pigments (Kreslavski et al., 2013a,b).

RL is the activation stimuli of phytochromes, the signaling of which increases the transient accumulation of transcription factors as well as Ca<sup>2+</sup> (second messenger) and H<sub>2</sub>O<sub>2</sub>, thereby leading to increased activity of antioxidant enzymes and more low-molecular-weight antioxidants (Kreslavski et al., 2013; Khudyakova et al., 2017).

It was demonstrated that *hy3* mutants are defective in the PhyB apoprotein and, thus, in PhyB, showing a 20–30-fold deficiency of PhyB transcripts in comparison with WT (Somers et al., 1991). In the absence of stress factor, the amounts of photosynthetic pigments and UV-absorbing components were lower in *hy3* mutants, compared to WT, although the PSII activity and the rate of net photosynthesis slightly differed among WT and *hy3* mutants. Moreover, PSII of *hy3* showed a lower level of resistance to UV-A stress, compared to the WT (Kreslavski et al., 2013; Kreslavski et al., 2016).

The development of chloroplasts and chlorophyll content were also compared in rice *PhyA*, *PhyB*, *PhyAPhyB* mutants, and WT. While *PhyB* mutants showed reduced chlorophyll content, mutation of *PhyA* resulted in a negligible reduction of chlorophyll content. The reduction of chlorophyll content in the double mutant, however, was more pronounced than *PhyB* mutants (Jie et al., 2013). Furthermore, *PhyA* and *PhyB* signaling networks took part in starch accumulation and controlled primary metabolism in *Arabidopsis* leaves in response to light (Han et al., 2017).

The content of specific phytochromes can also affect photosynthetic activity. In a study on the effect of continuous light injury on tomatoes, it was revealed that PHYA over-expression increased plant tolerance to continuous light (CL) regardless of the light spectrum. When the FRL spectrum of CL was reduced, the injury was diminished in PHYB1 and enhanced in PHYB2,

although the effects were small. This led to an understanding that phytochrome signaling networks take part in shaping responses to CL (Velez-Ramirez et al., 2019).

It was also revealed that plant responses to UV-C are PhyA- and PhyB-dependent. Their responses to UV-A are PhyA-dependent, to RL are PhyB-dependent, to BL are CRY1- and CRY2-dependent, and to UV-B are UVR8-dependent. The UV-B responsive genes were reportedly regulated via UVR8 and CRY1 in a COP1/HY5-dependent manner (Roerber et al., 2021).

Furthermore, the expression of PhyB apoprotein from *Arabidopsis* in transgenic cotton resulted in a four-fold increase in stomatal conductance and transpiration rate as well as a two-fold increase in net photosynthesis, compared to non-transgenic plants (Rao et al., 2011). Moreover, the stomatal density of *Arabidopsis thaliana* increased under a high RL/FRL ratio (Bergo et al., 2003; Boccalandro et al., 2009). In addition, a study on chrysanthemums showed that the size of stomata decreased, whereas their density increased in plants grown under RL (Seif et al., 2021). There was an involvement of PhyB in stomatal response and ROS-signaling under high light stress (Devireddy et al., 2020). Another study on the role of phytochromes in UV-induced programmed cell death (PCD) suggested the occurrence of PCD in response to impaired photosynthetic electron transport, depending on phyB and phyA signaling (Rusaczonk et al., 2015). Delicate interplays between ROS waves, phytochrome B, and excess light stress were also demonstrated (Devireddy et al., 2020).

### ***Production of grafted seedlings***

Grafted seedlings offer a large potential for producing horticultural plants. They are nowadays attracting the attention of horticulturists for cultivating vegetables. However, environmental factors during the healing and acclimatization stages of grafted seedlings are challenging for success in grafted seedling production (Moosavi-Nezhad et al., 2021). In this method, since the scion has no vascular connection with the rootstock in the first stage of grafting (healing), the scion is highly prone to desiccation. To prevent scion desiccation, based on the leaf water vapor pressure deficit response, relative air humidity should be kept very high (above 90%) and the vapor pressure deficit (VPD) should be maintained lower than 0.3 KPa to make a low evaporative demand force between the inner part of the leaf and the outside environment (Aliniaiefard and van Meeteren, 2013; Ngoc

Thang et al., 2013; Aliniaiefard and van Meeteren, 2016; Aliniaiefard and van Meeteren, 2018; van Meeteren and Aliniaiefard, 2016). Ultimately, this can minimize water loss and prevent scion wilting (Moosavi-Nezhad et al., 2021; Moosavi-Nezhad et al., 2022). In the traditional way of grafted seedling production, the healing and acclimatization are done under conventional tunnel systems covered by polyethylene plastic. Exposure to direct natural light is devastating for grafted seedling performance. However, lighting environments are less likely to be under proper control due to diurnal and seasonal changes. When the light intensity exceeds a certain level or even when the light quality is not properly handled, it would result in photoinhibition, excess water loss, and failure in the grafting practice (Rouphael et al., 2018; Moosavi-Nezhad et al., 2021). In a study by Moosavi-Nezhad et al. (2021), a vertical system equipped with LED lights was used during the healing and acclimation of watermelon-grafted seedlings. It was shown that producing grafted watermelon seedlings under red light led to photoinhibition on the leaf of the scion part, whereas blue light reduced the occurrence of photoinhibition in the watermelon grafted seedlings. Another study on the role of light quality on grafted tomatoes indicated that red and blue light mixture (R7:B3) increased total leaf area, dry weight (total, shoot and root), and total chlorophyll/carotenoid ratio. Moreover, this treatment enabled grafted seedlings to maintain a higher photosynthetic index (Gent, 2014).

### ***Production of in vitro plantlets***

There are many challenges to seed application in the propagation of horticultural plants. Some of these challenges include a long juvenility period, a long duration required to reach the commercial yield, high heterozygosity, and incompatibility (Grouh et al., 2011; Farsi et al., 2018; Thapa et al., 2021). To prevent these challenges, *in vitro* tissue culture has emerged as a promising, rapid, and large-scale method for the propagation of horticultural plants. Despite these advantages, *in vitro*-generated plantlets are extremely prone to stress when exposed to ex-vitro conditions, characterized by completely different environmental conditions than their habitant *in vitro* counterparts. This problem can be regarded as a major limitation of plant propagation *in vitro* (Pospisilova et al., 2007; Eshghi Khas et al., 2020). *In vitro* environments are characterized by extremely high relative humidity levels or very low vapor pressure deficits (VPDs). It has been reported that plants produced/exposed in/to

high relative humidity or low VPD conditions develop some morphological, anatomical, and physiological disorders. These disorders or abnormalities are causes or consequences of poor photosynthetic functionality, abnormal stomatal characteristics and functionality, as well as limited cuticular development on the leaves (Rezaei Nejad and van Meeteren, 2012; AliniaEIFard and van Meeteren, 2013; Asayesh et al., 2017a,b). Since tissue-cultured plants are supplied with an adequate source of sugars *in vitro*, along with a low light intensity on plant materials *in vitro*, it is generally accepted that photosynthesis does not have a prominent role in the growth of *in vitro* plant materials (heterotrophic condition). However, some studies have advocated the important role of photosynthesis *in vitro*. For instance, in a study on Liliium plants, CO<sub>2</sub> was removed from the culture vessels that were supplied with sugars. Removal of CO<sub>2</sub> resulted in a substantial decline in the maximum quantum efficiency of photosystem II (F<sub>v</sub>/F<sub>m</sub>) (Askari et al., 2022). This is indicative of the occurrence of photoinhibition under limited CO<sub>2</sub> concentrations and the importance of photosynthetic functionality among *in vitro* plantlets. In general, tissue-cultured samples have lower F<sub>v</sub>/F<sub>m</sub> than *ex-vitro* plants, which is indicative of immature development of the photosynthetic system. They are very sensitive to high light intensities and evaporative demands thereafter. It has also been confirmed that the application of photoautotrophic conditions, by increasing light intensity and CO<sub>2</sub> concentration, can help *in vitro*-produced plantlets develop a functional photosynthetic system, capable of better acclimation to the *ex vitro* environment (Yamashino et al., 2013; Askari et al., 2022).

## Conclusion

In this review, we provided a brief introduction to the main horticultural production systems that involve prone crops to photoinhibition and photoprotection mechanisms. We explained how different aspects of light may trigger plant production in greenhouses or CEH systems. In addition, the impacts of other environmental factors on plant responses to light were mentioned. Then, we discussed the possible roles of light quality and signaling (as they are frequently manipulated in the CEH systems) in photoinhibition and photoprotection. The information provided in this paper can be a general guide for achieving a well-tuned protocol for the provision of light to systems of plant production. Thus, this study is an important step to pave the way toward breeding horticultural

crops and making them more suitable for production in the CEH systems.

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