

Regulation of Photoassimilate Distribution between Source and Sink Organs of Crops through Light Environment Control in Greenhouses

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Abstract

Photosynthesis, the most important physiological process in plants, can produce not only ATP and NADPH used in other processes but also carbohydrate, the key factor for crop yield. Production of photoassimilates is often influenced by various environmental factors such as light, temperature, CO₂, water, mineral elements and leaf stage and position. Here we focused on the light-mediated regulation of photoassimilate translocation in plants and the application of light environment control in greenhouse production. We also reviewed the effects of other factors including leaf age and position, air temperature, CO₂ concentration and water and mineral element supply on photoassimilate translocation in plants. Finally some perspectives have been proposed.

Keywords

Light; Photoassimilate Translocation; Plant

1. Introduction

As sessile organisms, plants may suffer from many unfavorable environmental conditions such as drought, mineral insufficiency, low light intensity and chilling, which all can significantly influence their growth and productivity via disturbance of the normal physiological processes in plants. In these processes, capacity to produce

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high amounts of photoassimilates and efficient partitioning of carbon compounds towards harvestable organs have been shown a major impact on crop yield [1] [2]. Therefore, a series of studies on the relationship between environmental factors (e.g. light, air temperature, relative humidity and CO₂ concentration) and crop production have been done to optimize the environmental conditions for stimulating photoassimilate translocation to harvestable organs. Among these environmental factors, light is thought to be the most important one. Here, recent advances about the involvement of light environment, including light intensity, photoperiod and light quality, in photoassimilate translocation have been reviewed. Supplemental lighting is thus considered as a powerful approach and has been applied widely in greenhouse production to improve crop yield and quality. In addition, the effects of leaf stage and position, air temperature, CO₂ concentration and water and mineral element supply have also been introduced on the partitioning of photosynthetic product from source to sink organs in plants. Finally some perspectives in this field have been proposed as well.

2. Light Environment and Photoassimilate Translocation

2.1. Light Intensity

Light intensity is a fundamental factor for the translocation of photoassimilates in plants. The export percentage of carbon from source leaves is stable, but the amount of carbon per unit leaf area mainly depends on the carbon pool [3]. The carbon pool of a leaf is determined by light intensity, leaf photosynthetic capacity and leaf features such as area and thickness [4]. Robbins and Pharr reported that the photoassimilate translocation from leaves of cucumbers is significantly promoted with alteration of light intensity from 380 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ to 650 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ [5]. Nishizawa *et al.* reported that the amount of carbon exported is higher in tomato seedlings raised under 414 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ than those raised under 166 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ PPF [3]. The reason for these differences in photoassimilate translocation might be attributed to both the direct positive effects of light intensity on the activities of enzymes related to photoassimilate translocation and its indirect positive effects on stomata opening [6] [7].

2.2. Photoperiod

The influence of photoperiod on partitioning of photoassimilates between soluble sugar and starch is considered to determine the concentrations of carbohydrate available for growth of sink organs [8]-[10]. Previous studies showed that the extension of photoperiod can significantly increase the export of photoassimilates from source leaves to sink organs [5] [11]. This can be explained by the results of recent proteomic analysis, which uncover that enzymes involved in reduction phase of Calvin-Benson cycle are more abundant in plants under long day treatment than those under short day treatment [12]. However, it does not mean “the longer, the better”. Moe *et al.* reported that continuous lighting (24 h) results in reduced yield and serious leaf yellowing of cucumbers [13].

2.3. Light Quality

Translocation of photoassimilates in crops also responds to light quality. Compared with broad spectrum ones such as daylight fluorescence lamp, red-biased light sources such as high pressure sodium (HPS) lamp enhance carbohydrate levels in the leaves of *Digitaria decumbens* and *Asplenium australasicum* [14] [15]. Blue light can stimulate the accumulation of photoassimilates in cucumber source leaves, while photoassimilate export is significantly increased to sink organs by red light [16]. The stimulation of photoassimilate translocation from source leaves to fruits by UV-B light has also been reported [17]. All evidence indicates that the influence of light quality on photoassimilate translocation might be specie-specific.

2.4. Supplemental Lighting

In winter, natural light intensity level is too low to produce fruit vegetables in the region of rigid and temperature zones. Therefore, artificial light has been applied to improve light environment in crop canopy. Now supplemental lighting is an important technology in greenhouse production in the region of middle and high latitudes [18]-[21]. Supplemental lighting is almost exclusively applied on the top of crop canopy (**Figure 1**). However, top lighting (TP) might not be the optimal, because it provides unequal irradiation distribution, with the top of the canopy receiving more irradiation than the lower parts [22]. Consequently, the lower leaves may at times be below light compensation point, while the upper leaves may be approaching the saturation point of photo-

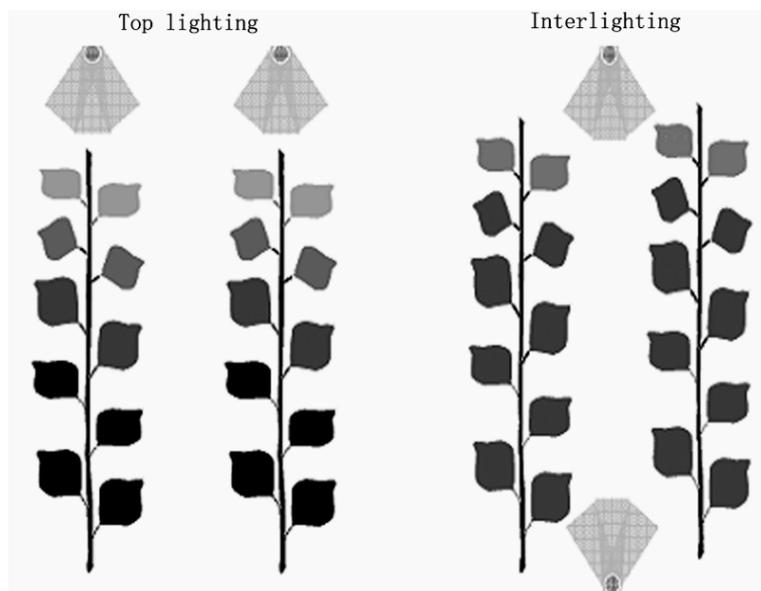


Figure 1. Models for top lighting and interlighting in greenhouses.

synthesis [22]. The insufficient supply of photoassimilates, which results in the competition for assimilates between fruits and vegetative organs, is considered to be an important reason for fruit abortion and retarded growth, which severely influence cucumber yield [23]. Interlighting (IL), which means that part of supplemental lighting is installed between crop rows instead of completely on the top of crop canopy (Figure 1), has raised interests not only among researchers but also among growers of greenhouse vegetables in recent years [24]. Many horticultural crops such as tomato and cucumber have been shown to benefit from interlighting because of the increase of photoassimilate supply from the leaves at the bottom layer (Table 1).

3. Other Factors for Photoassimilate Translocation

3.1. Leaf Age and Leaf Position

Nishizawa and Hori investigated the effects of leaf age and position on photoassimilate translocation from leaves of strawberry plants at the vegetative stage [27]. The results showed that the export of ^{14}C -assimilates increases with the increase of leaf age and reaches to the peak at 40 days after full expansion. In the strawberry plants with 7 fully expanded leaves, where Leaf-7 is the uppermost, the contribution percentage to the total production of photoassimilates is the greatest for Leaf-5 followed by Leaf-6, although the photosynthetic capacity differs little from Leaf-1 to Leaf-5 and is somewhat lower in Leaf-6 and Leaf-7. These variations might be associated with light intercepting efficiency of individual leaf at different nodes.

3.2. Air Temperature

Translocation of photoassimilates in crops is largely influenced by air temperatures [28] [29]. Toki *et al.* reported that during dark period photoassimilates in mature cucumber leaves are exported within 2 h at 20°C and 4 h at 16°C of air temperature [30]. At 10°C of air temperature, translocation of photoassimilates is strongly inhibited. Miao *et al.* reported that compared to cucumbers grown at 22°C of night air temperature, sucrose, stachyose and galactinol contents increase in mature leaves, while sucrose, glucose and fructose contents in fruits remain unchanged at 12°C [31]. In peduncles, where stachyose is catabolized to sucrose after long-distance transport, cold night simultaneously induces a significant increase of stachyose and a decrease of sucrose, indicating that the metabolic step from stachyose to sucrose is significantly inhibited in peduncles of cold-night grown cucumbers.

3.3. CO₂ Concentration

Positive effects of CO₂ availability on plant growth and development have been reported in previous studies

Table 1. Effects of different lighting regimes on crop production.

Crops	Treatment	Light sources	Results	References
Cucumber	TL/TL + IL	HPS lamp	Significant increase of yield and improvement of fruit quality by TP + IL.	[22]
Tomato	TL/IL	HPS lamp for TL, LED lamp for IL	Significant increase of electrical conversion efficiency by IL.	[25]
Mini-cucumber	TL/TL + IL	HPS lamp for TL, LED lamp for IL	Significant increase of yield at early production period and improvement of fruit visual quality by TL + IL.	[26]

[32]. Peet *et al.* reported that cucumber leaf starch concentration, sucrose synthase (SS) and sucrose phosphate synthase (SPS) activities are higher under 1000 $\mu\text{mol mol}^{-1}$ of CO_2 concentration than those under 350 $\mu\text{mol mol}^{-1}$ [33], indicating that the increasing of CO_2 concentration might have positive effects on photoassimilate translocation in cucumbers. Some negative effects by CO_2 enrichment on plants have also been reported due to the disturbance of the balance between nitrate and carbon metabolism at the same time [34].

3.4. Water and Mineral Elements

The supply of water and mineral elements can be involved in the regulation of photoassimilate translocation from source to sink organs of plants as well. Water deficiency is an important factor restricting crop development and yield. Mild water deficiency inhibits shoot growth only and, consequently, can cause plant architecture modification [35] [36]. As a result of this modification, net photosynthesis may decrease and thus the photoassimilate translocation to different sink organs is affected [37]. Mineral deficiency can stimulate photoassimilate translocation from source leaves to mineral element acquisition organs either directly through the enhancement of phloem loading and transport or indirectly through the depression of the need of other sink organs [38]. Consequently, a larger root surface and higher sugar concentration can be observed in plants under mineral element deficiency [39] [40]. However, it is still unclear whether the increased sugar concentration is a stress response and/or a stress signal [37].

4. Conclusions and Future Prospects

Light is critical for the synthesis and translocation of assimilates from mature leaves to harvestable organs of greenhouse crops. Light environment can be controlled through adjustment of light intensity, photoperiod and light quality by supplemental lighting, which now has become an effective technology for the production of vegetables, fruits, flowers and so on. But there are still some problems which limit the application of light environment control in greenhouse production.

The basic knowledge about light-mediated photoassimilate translocation in plants is still poor because of the remaining ambiguity in the underlying mechanism of source-sink relationship and its interaction with environmental factors. For example, a mismatch between the increase in photosynthesis by supplemental lighting and the increase in resulted yield has been widely reported in previous studies due to the deficiency of sink capacity to fully utilize the increased supply of photoassimilates [41]. Hence, actual crop yield in a given crop-season depends on a complex interplay of light interception, photosynthetic efficiency, sink strength and harvest index. There is ample evidence of heritable variations between different crops and between different cultivars for the characters of light interception, photosynthetic efficiency, sink strength and harvest index, but yet there are still few studies that report the genetic basis of these characters either individually or in combination. If the underlying mechanism for this complex interplay can be illuminated, we can better understand the source-sink relationship in plants and thus optimize the present light environment control technology.

The defects in present supplemental lighting systems are restricting the further application of light environment control technology in greenhouse production as well. The most significant factor is the high capital cost for the design and installation of artificial lighting systems in greenhouses, especially in developing countries such as China. Another problem is that the light spectrum of present artificial light sources such as HPS lamp is not well consistent with the optimal light spectrum of photosynthetic pigments [42]. This mismatch reduces the utilization efficiency of artificial lighting and thus increases the production cost in greenhouses. In order to extend the application of artificial lighting in greenhouse production, people should reduce the price of the present

lighting systems through technique innovation and develop new artificial light sources which can be well consistent with plant needs. LED lamp is a kind of solid artificial light source with longer lifespan, less heat emission and narrower spectrum compared with the traditional lamps and recently has been introduced into greenhouse production [43]-[45]. In theory we can develop lighting systems with optimal spectrum for specific crops through combination of different LED lamps, but still there are few studies about how LEDs are combined and how crops respond to these combinations.

Light environment control can be realized not only by supplemental lighting but also by cover materials such as plastic film and shade net in greenhouses [46]. Especially in middle-latitude or low-latitude areas such as Central China and South China, cover materials might be a more economic approach than supplemental lighting because light intensity in these areas is enough to grow most of horticultural crops in greenhouses even in winter. However, environmental changes including not only light but also temperature and relative humidity in greenhouses by cover materials are much more complex than those in greenhouses with supplemental lighting [47] [48]. As a result, the responses of crops might be quite different to cover materials from those to artificial light sources. More studies should thus be done in order to promote the application of functional cover materials in greenhouse production in the future.

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