

# Chapter 8

## Optical and Physiological Properties of a Leaf

**Keach Murakami and Ryo Matsuda**

**Abstract** The most important role of a leaf is capturing light energy and fixing CO<sub>2</sub> into carbohydrates (i.e., photosynthesis). Fundamental knowledge on the optical and physiological properties of an individual leaf of a C<sub>3</sub> plant is summarized below. A leaf adjusts light absorption, at the scales of both whole-leaf and intra-leaf, in order to efficiently capture light energy and to avoid photodamage caused by excessive light energy. Several interacting factors involved in orchestrating these optical properties, such as leaf orientation, mesophyll structure, chloroplast movement, and the absorption properties of phytopigments, are outlined. Photosynthesis consists of two reactions that are spatially separated within the chloroplast. Light energy is converted into reducing power and chemical energy via the electron transport chain. These are then consumed during CO<sub>2</sub> fixation in the carbon assimilation process. The electron transport reaction is affected significantly by the spectral distribution of light due to the optical properties of the leaf. Photosynthesis is closely related to other physiological processes. CO<sub>2</sub> uptake accompanies water vapor release (transpiration). Produced photosynthates are transported to the other plant organs (translocation). Brief information about the significance and the machinery of these photosynthesis-related processes is provided.

**Keywords** Carbon assimilation • Electron transport • Light absorption • Photosynthetic quantum yield • Phytopigment • Transpiration • Translocation

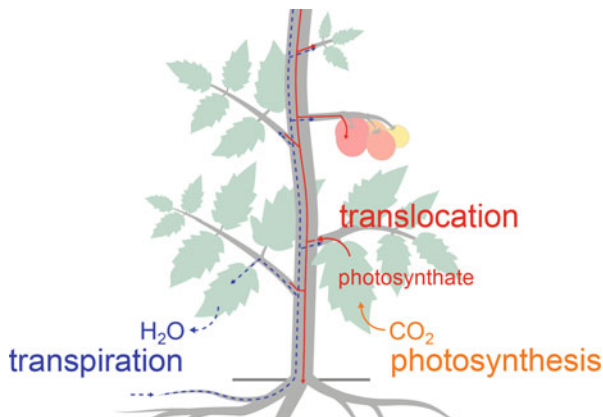
### 8.1 Introduction

The most important role of a leaf is capturing light energy and fixing CO<sub>2</sub> into carbohydrates—i.e., photosynthesis—and serving them as the energy source to the plant. In greenhouses and plant factories, LEDs are used to enhance the photosynthetic rate of plants, as well as to regulate development, such as floral differentiation

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K. Murakami (✉) • R. Matsuda  
Graduate School of Agricultural and Life Sciences, The University of Tokyo, Bunkyo-Ku,  
Tokyo, Japan  
e-mail: [keach.murakami@gmail.com](mailto:keach.murakami@gmail.com)

**Fig. 8.1** Schematic diagram of leaf functions and flows of photosynthate (solid lines) and water (dashed lines) in plants



and morphogenesis. The aim of this chapter is to outline the optical properties and photosynthetic physiology of a leaf in a  $C_3$  plant. A leaf is a site not only for photosynthesis but also for other physiological processes, such as transpiration and translocation, which are essential for maintaining efficient leaf photosynthesis (Fig. 8.1). Brief information about the significance and the machinery of transpiration and translocation will be provided in connection to photosynthesis. These physiological functions of a leaf are variable in response to changes in environmental factors, such as photosynthetic photon flux density (PPFD), air temperature, relative humidity,  $CO_2$  concentration, and air current. The close relationships between leaf physiology and environmental factors will be reviewed in the following chapters. Some other physiological responses, such as respiration and senescence, occur commonly in plant cells (not uniquely in leaf cells) and are beyond the scope of this work.

## 8.2 Optical Properties of a Leaf

An individual leaf has several mechanisms that function to capture light efficiently. A leaf also has several mechanisms to dissipate any excess energy from incident light, in order to avoid photodamage. In this section, we will introduce how a leaf regulates the absorption of incident light and the vertical profiles of PPFD and spectral distribution of light within the leaf. Then we will describe the general functions of phytopigments and their light absorption properties, which originate the leaf absorption spectrum. The vertical light profiles within a leaf, as outlined in this section, are analogous to that observed in plant canopies and communities (see Chap. 9 for more details).

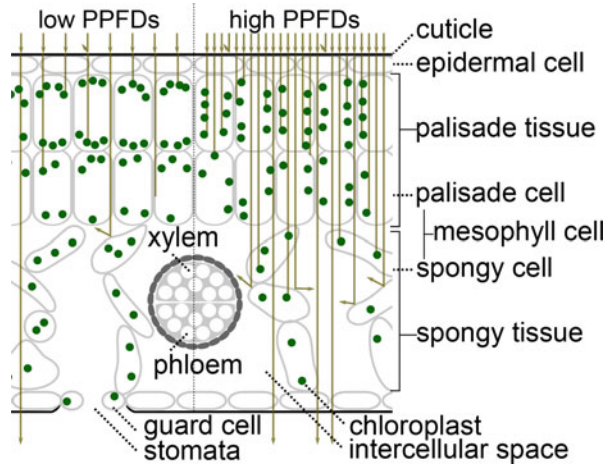
### 8.2.1 Leaf Orientation and the Vertical Light Profiles Within a Leaf

A leaf changes its orientation in response to the incident light angle from a light source. This light-tracking movement, namely, heliotropism, contributes to maximizing light capture while avoiding excess light energy absorption (Muraoka et al. 1998). These leaf movements have been proven to be mediated by blue light (BL) photoreceptors in *Arabidopsis thaliana*, a model plant species (e.g., Inoue et al. 2008).

Light reflection properties on a leaf surface also change in association with the change in leaf angle (e.g., Brodersen and Vogelmann 2010). A large proportion of photons, those not reflected by the leaf surface, enter the leaf. Note that a portion of the light that enters the leaf is reflected by the numerous air/cell interfaces and exits from the leaf without being absorbed (Vogelmann 1993). A dorsiventral leaf consists of vertically differentiated two-layer mesophyll tissues (palisade and spongy tissues) sandwiched between epidermal cells (Fig. 8.2). The epidermis is covered with a waxy covering called the cuticle, which protects against water evaporation and pathogen infection. The palisade cells are cylindrically shaped, vertically elongated, and closely arranged along the upper epidermis. Chloroplasts play a central role in photon absorption as they contain the photosynthetic apparatus and are the site of photosynthesis (see Sect. 8.3.1) in the mesophyll cells. The PPFD at a given paradermal plane decreases exponentially according to the depth within the mesophyll layers, and a large proportion of the photons is absorbed by the palisade chloroplasts (e.g., Brodersen and Vogelmann 2010). Light that penetrates the palisade layers enters the spongy layers. The spongy cells are loosely packed below the palisade tissues. Owing to the complex shape of spongy cells, the light is well scattered and the optical path is lengthened (Vogelmann 1993). The longer path length contributes to an increased opportunity for light absorption by the pigments.

The chloroplasts accumulate at the upper and lower sides of palisade cells at low PPFDs and redistribute on the side walls of palisade cells at high PPFDs (Fig. 8.2), as mediated by the BL photoreceptor phototropin 2 (Wada 2013). Under high-PPFD conditions, the chloroplasts in the upper cell layers absorb enough photons to become light saturated. Therefore, increasing photon absorption by these chloroplasts does not enhance whole-leaf photosynthesis. In this case, distributing light toward the chloroplasts in the lower cell layers enhances the whole-leaf photosynthesis, because these chloroplasts are not yet photosynthetically light saturated. In addition to the vertical distribution of the light, the photosynthetic characteristics of the chloroplasts also exhibit a vertical profile within a leaf (e.g., Terashima et al. 2009). For better comprehension of the vertical light profiles within a leaf and photosynthetic properties of a leaf, see Terashima et al. (2009) and the cited articles therein.

**Fig. 8.2** Vertical cross section of a leaf and the distribution of chloroplasts at high and low PPFDs

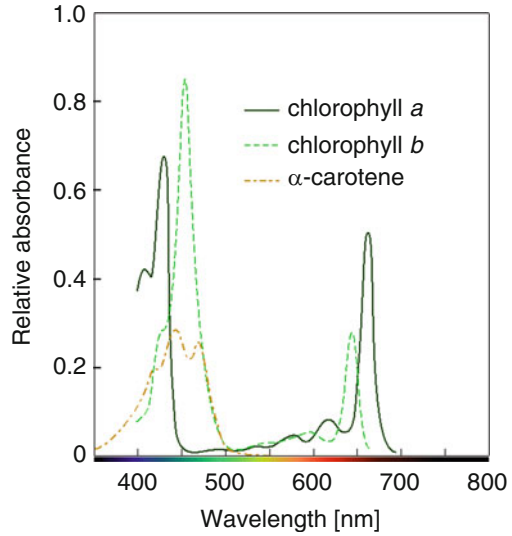


## 8.2.2 Pigments and Spectral Absorption of a Leaf

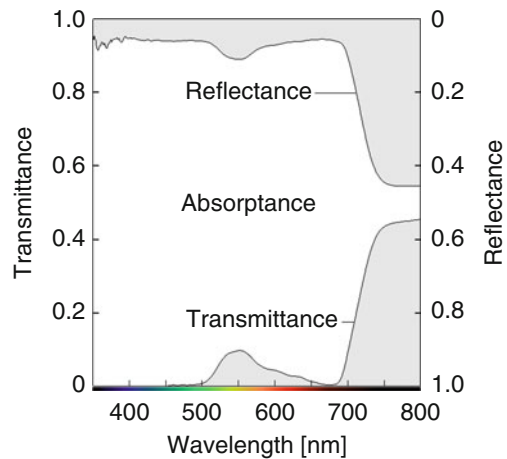
As they travel through the leaf, photons are absorbed by phytopigments. The representative pigment of photosynthetic organisms is chlorophyll (Chl). In higher plants, two types of Chls (Chl *a* and Chl *b*) play a dominant role in photosynthetic light absorption. The absorption peaks of these pigments are observed in the blue and red wavebands (Fig. 8.3). A portion of the energy of photons absorbed by Chls is consumed by photochemical reactions (see Sect. 8.3.1). Other pigments are also involved in photosynthetic photon absorption in a leaf. Some carotenoids—insoluble pigments in chloroplasts with an absorption band ranging approximately 350–500 nm (Fig. 8.3)—absorb photons and transfer the energy to Chls. Owing to this function, they are called accessory pigments. On the other hand, at high PPFDs, different types of the carotenoids receive a certain amount of energy from Chls and dissipate it as heat. This system (xanthophyll cycle) protects the photosynthetic apparatus from photodamage (Niyogi et al. 1997). Another major phytopigment group is the flavonoids like anthocyanin mainly accumulating in the vacuole of epidermal cells. Flavonoids absorb shorter wavelengths of light, including ultraviolet (UV) radiation, but the energy is not utilized for photosynthesis. The main functions of flavonoids are cell protection by the screening of UV radiation from incident light and the deactivation of reactive oxygen species (Agati and Tattini 2010). The BL photoreceptor cryptochrome 1 is reported to be involved in the expression of genes related to flavonoids biosynthesis in *Arabidopsis* (Jackson and Jenkins 1995).

As a result of the spectral absorption properties of the pigments, light absorbance of a leaf depends on the wavelength of the light (Fig. 8.4). Note that the term absorbance ( $\alpha$ ) indicates the fraction of light absorbed, while absorbance ( $A$ ) indicates the attenuation of the light in the logarithmic scale. These parameters can be defined at a given wavelength as

**Fig. 8.3** Absorbance spectra of chlorophyll *a* and *b* and  $\alpha$ -carotene (Adapted from Gates et al. 1965)



**Fig. 8.4** Absorbance, reflectance, and transmittance spectra of a cucumber leaf (Adapted from Murakami et al. 2016)



$$\alpha = \frac{I - (I_R + I_T)}{I}, \quad \text{and} \quad A = -\log_{10} \left( \frac{I_T}{I} \right)$$

where  $I$ ,  $I_R$ , and  $I_T$  are spectral photon flux densities (PFDs) or irradiance of incident, reflected, and transmitted light, respectively. Because of the fundamental principle of light absorption (the Beer-Lambert law), the absorbance is in proportion to the optical path length and the concentration of the pigments. As shown in Fig. 8.3, the in vitro absorbances of the photosynthetic pigments in the green waveband are quite low. The low absorbances result in a higher proportion of PFD in the green waveband in reflected light; thus, a leaf generally looks green.

However, although the absorbances are very low, a considerable proportion of the photons in the green waveband is still absorbed by a leaf (Fig. 8.4). This is because the remarkably elongated optical path length, caused by the scattering effect, increases the opportunity of photon absorption in the green waveband (Terashima et al. 2009). Considering these data, the extent to which green light (GL) actually drives photosynthesis of a leaf is greater than what is inferred from the pigment absorbance spectrum and the leaf color. Moreover, the lower absorbance in the green waveband indicates that GL can reach chloroplasts located in cells deeper within the leaf, more so than BL and red light (RL), as shown by Brodersen and Vogelmann (2010). GL might enhance the leaf photosynthetic rate by increasing the photosynthetic rate of the chloroplasts located in the lower cells, i.e., those that are not yet photosynthetically light saturated, when the upper mesophyll chloroplasts are light saturated (Terashima et al. 2009).

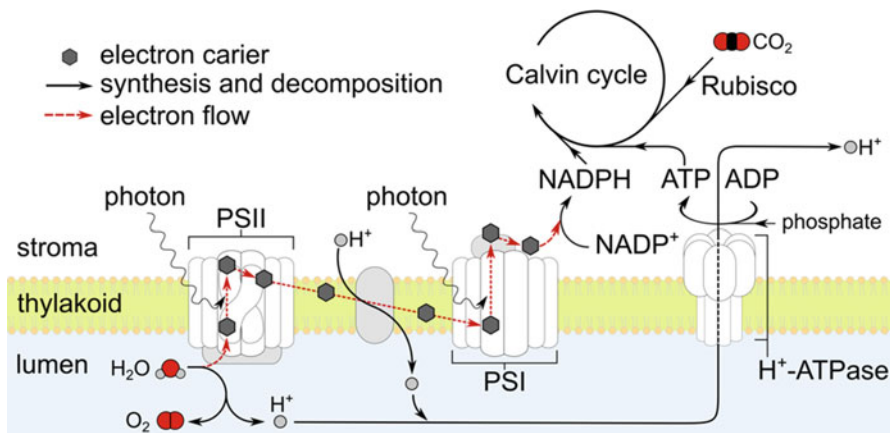
Even with the relatively planar leaf absorptance spectrum resulting from the scattering effect, the transmitted incident light on the lower leaves still contains more GL and far-red light (FRL) than does untransmitted light. The relative spectral PFD distribution, especially in the far-red waveband, seems to be used by plants as the key stimulus for inducing changes in photosynthetic characteristics (i.e., light acclimation) of the irradiated leaves (e.g., Murakami et al. 2016) and in whole-plant growth (Demotes-Mainard et al. 2015). The light environment of a leaf not only affects the photosynthetic characteristics of the irradiated leaf but also those of unirradiated, newly developing leaves (e.g., Murakami et al. 2014). In higher plants, environmental changes around an organ sometimes induce morphogenetic and physiological reactions not only to the organ but also to other parts of organs. Such phenomena are called systemic regulation.

### 8.3 Physiological Properties of a Leaf

Considering the above mentioned light absorption properties of a leaf, we will now outline the machinery of photosynthesis. We will pay particular attention to the light-driven process of photosynthesis and its dependency on spectral PFD distribution, due to the importance in the horticultural application of LEDs. We also briefly summarize the importance and the machinery of transpiration and translocation in this section, as representative photosynthesis-related physiological processes.

#### 8.3.1 *Photosynthesis*

Photosynthesis consists of two reactions that are spatially separated within the chloroplast (Fig. 8.5): (1) light-driven electron transport on the thylakoid membrane (the lipid bilayer within the chloroplast) and (2) enzymatic reactions for carbon



**Fig. 8.5** Schematic diagram of the photosynthetic electron transport reactions on the thylakoid membrane and carbon assimilation in the stroma of a  $C_3$  plant

assimilation in the stroma (the fluid surrounding the thylakoid membranes within the chloroplast). The reducing power and chemical energy produced by electron transport are consumed during the carbohydrate synthesis of the carbon assimilation. An appropriate balance between these two reactions is essential for efficient photosynthesis. These have traditionally been called the “light reaction” and the “dark reaction”, respectively. However, further research has clarified that several processes in the light reaction progress without light and that a part of the dark reaction needs light in order to activate some of the necessary enzymes. Thus, these terms are not currently accepted. Though the terminology seems to be under discussion among the specialists, we will use the terms “electron transport” and “carbon assimilation” to avoid confusion in this chapter.

*Electron Transport* The light energy captured by Chls and accessory pigments is converted into reducing power as the reduced form of nicotinamide adenine dinucleotide phosphate (NADPH) and chemical energy as adenosine triphosphate (ATP), through the electron transport chain (ETC). The ETC is anchored by the two photochemical reactions, occurring in series, at the two photosystem complexes, PSII and PSI, within the thylakoid membrane (Fig. 8.5). The electron transports are powered by photon energy transferred to the respective photosystems, thus enabling electron transfer against the redox potential (called the Z scheme). The series of the two reactions drive (1)  $O_2$  evolution, proton ( $H^+$ ) production in the lumen (the fluid inside of the thylakoid membrane), and electron ( $e^-$ ) subtraction, by water decomposition, (2) transfer of the electron via carriers and accompanying  $H^+$  movement from stroma to lumen, and (3)  $NADP^+$  reduction into NADPH by consumption of the electrons. The accumulated protons in the lumen form a pH-gradient across the membrane. This electrochemical potential drives ATP synthesis from adenosine diphosphate (ADP) and phosphate, via  $H^+$ -ATPase in the membrane. As the results

of ETC, NADPH and ATP are generated in the stroma. These end products are used widely as a reductant and an energy source, respectively, in plant metabolism.

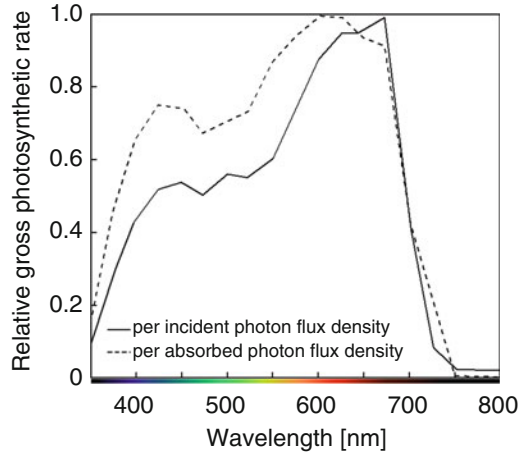
Because of the optical properties of a leaf (see Sect. 8.2), the gross photosynthetic rate of a leaf ( $P_g$ ) also depends on the spectral PFD distribution of light (e.g., McCree 1972, Inada 1976). When a leaf surface is irradiated with light at the same PFD incident, the  $P_g$  is highest in the red waveband, followed by the blue and then the green wave bands (solid line in Fig. 8.6). Note that FRL and UV, which deviate from the definition of photosynthetically active radiation (PAR), also drive photosynthesis slightly. Even when  $P_g$  is represented per unit of absorbed photons by a leaf (photosynthetic quantum yield) to compensate for the differences in absorptance, yield is still dependent on the wavelength (dashed line in Fig. 8.6). The quantum yield in the green waveband is comparable to that in blue, indicating that GL moderately drives the ETC when absorbed. The relatively lower quantum yields in the blue and green wavebands, compared to the red wave band, should be attributable to the absorption by the non-photosynthetic pigments (flavonoids) and to the heat dissipation by the carotenoids.

As for the longer wavelengths (>680–690 nm), the quantum yield decreases sharply. This sharp decrease can be accounted for by the difference in the light absorption properties between PSII and PSI. PSI contains much Chl *a* and thereby preferentially absorbs longer wavelength of light than PSII absorbs (e.g., Evans 1986). Because of this preferential absorption by PSI, electron transport is limited by the lower electron transport reaction rate of PSII. Under this condition, photon absorption by PSI exceeds supply, and the light-use efficiency of the reaction in PSI is hence lowered. In contrast, BL and RL have been reported to be preferentially absorbed by PSII (e.g., Evans 1986). Therefore, a measured quantum yield under the mixture of FRL+RL or FRL+BL can be higher than that estimated from the separately obtained yields (Emerson effect).

*Carbon Assimilation* Dissolved CO<sub>2</sub> in the stroma is fixed into sugar phosphates. This carbon assimilation process, called the Calvin cycle, consists of over a dozen enzymatic reactions. The most important and abundant enzyme in the Calvin cycle is ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). This enzyme catalyzes the entry-point reaction of CO<sub>2</sub> into the cycle. Triose phosphate (TP), the end product of the Calvin cycle, is synthesized from the fixed CO<sub>2</sub>, consuming the NADPH and ATP produced by the ETC. A portion of the TP created is exported to the cytosol and converted into sucrose. TP is also required for starch synthesis in the chloroplasts. At the same time, Rubisco catalyzes the oxygenation reaction, consuming O<sub>2</sub>. This reaction triggers a series of enzymatic reactions wherein CO<sub>2</sub> is released and NADPH and ATP are consumed (the glycolate cycle). Although the physiological role of this process is still debated, these reactions decrease the photosynthetic carbon assimilation rate and photosynthetic light-use efficiency (see also Chap. 12).



**Fig. 8.6** Relative gross photosynthetic rates per incident (*solid line*) and absorbed (*dashed line*) photons. The mean values of 22 plant species are shown (Adapted from McCree 1972)



### 8.3.2 Transpiration

Transpiration is the process of water vapor movement from plants to the atmosphere. Although transpiration can occur at any aerial part of the plant, such as stems and flowers, leaves are the predominant organ for transpiration.  $\text{CO}_2$  uptake occurs at the expense of inevitable water vapor release in leaves. The amount of  $\text{H}_2\text{O}$  molecules released from plant tissues is approximately 500 times as many as that of  $\text{CO}_2$  molecules taken in during this gas exchange. Through transpiration, water vapor diffuses along the concentration gradient between the transpiring surface of the plant and the atmosphere. The water vapor moves through stomatal pores or across the cuticle layer (called stomatal or cuticular transpiration, respectively). In stomatal transpiration, water vapor evaporates at the surface of mesophyll cells, diffuses in the intercellular air spaces, and moves to the outside of the leaf through stomata located within the leaf epidermis. The flux of water vapor in this pathway is largely regulated by the extent of the stomatal openings. In cuticular transpiration, water vapor from the epidermal cell surface diffuses across the cuticular layer to the atmosphere. In either pathway, water vapor present immediately outside of the leaf surface further diffuses through the leaf boundary layer—a layer of boundary air flow formed on the leaf surface—to the “free” atmosphere (see Chaps. 12 and 13 for more details).

Too much transpiration can result in growth inhibition due to water shortage. Although there is the risk of wilting, this water movement process plays essential roles in plant growth. First, it serves as a driving force of the transpiration stream in the xylem, contributing to the absorption of water and inorganic ions from the root zone and to the transportation of water, ions, and organic compounds, such as phytohormones, throughout the plant. Thus, too little transpiration can lead to nutrient deficiency disorders.

Some of the major problems observed in greenhouses and plant factories are blossom-end rot in tomato fruits (e.g., Ho 1999) and tipburn in the leaves of lettuce (e.g., Collier and Tibbitts 1982) and strawberry (e.g., Bradfield and Guttridge 1979); these are caused by low concentrations of calcium in the cells. Promotion of transpiration by controlling vapor pressure deficit (VPD) and air current might be a key solution for these disorders (e.g., Goto and Takakura 1992). Second, transpiration contributes to leaf cooling by facilitating evaporative heat transfer. The leaf dissipates a part of the absorbed radiant energy so as not to overheat. The water vapor released by transpiration removes the energy as latent heat and suppresses the temperature increase of a leaf. Owing to the smaller thermal radiant intensity of LEDs in general lighting applications, leaf and plant temperatures can be kept lower than when using traditional light sources such as high-intensity discharge lamps (HIDs) and fluorescent lamps (FLs).

### 8.3.3 *Translocation*

The photosynthates manufactured in the leaf are transported to other organs as sucrose dissolved in phloem sap. This transportation through the phloem, called translocation, is usually explained by the pressure flow model (Münch 1930). The term translocation also indicates inorganic nutrition transport and/or cell-to-cell short-distance transport of the substrates in the broad sense, but we only refer to the long-distance sugar transport here. The organs that demand the substrates, such as the newly growing stems, leaves, flowers, fruits, and tubers, are referred to as “sinks”, while those supplying them (i.e., mature leaves) are “sources”. The translocated sucrose is converted into monosaccharides, and these are consumed as respiratory substrates to generate ATP and carbon skeletons. In fruits and storage organs, a portion of the sucrose is converted into starch and stored.

When the rate of photosynthate production exceeds the translocation rate, the produced photosynthates accumulate in the source leaves. Such a carbohydrate accumulation can be observed in particular during the day with a high PPFD. The accumulated photosynthates are reported to suppress instantaneous leaf photosynthesis and the synthesis of photosynthetic proteins such as Rubisco (e.g., Araya et al. 2006). The appropriate management of the balance between the source and sink has been believed to be important for maintaining a higher photosynthetic rate and enhancing the yields and quality of the harvests. A review article on this balance, dealing with tomato, is available (Ho 1988).

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