論文の内容の要旨

生物・環境工学専攻
平成 26 年度博士課程進学
氏名: 村上 貴一
指導教員: 富士原 和宏

論文題目

Analysis of light spectrum effects on photosynthetic electron transport based on excitation energy distribution between photosystem I and II

(光合成電子伝達に光質が及ぼす影響の光化学系 I ・ II 間の励起エネルギー分配に基づく解析)

Chapter 1. General introduction

The spectral distribution (SD) of light is a determinant of the light-dependent photosynthetic reaction rate, or electron transport rate (ETR). Even though the amount of absorbed photons is the same and under a strictly light-limited condition, the ETR depends on the SD (e.g. Emerson and Lewis 1943). That is, the relative SD (RSD) of light affects the intrinsic ETR. This RSD-dependency of the ETR is found to originate from the distribution of excitation energy (EE) between two photosystems (PSII and PSI) and the serial photosynthetic electron transport through these photosystems (e.g. Evans 1986).

Previous studies have provided qualitative knowledge on the distribution of EE and electron transport in response to the RSD of light. It is believed that a leaf maintains a higher ETR by functioning multiple systems in response to the RSD of light thereby adjusting the distribution of EE (e.g. Dietzel et al. 2008). However, little is known about the quantitative contributions of respective systems to the adjustments of the EE distribution. To elucidate the light acclimation of photosynthesis in response to the RSD of light, quantitative analyses of the adjustments of the distribution of EE in connection with their influence on the ETR are necessary.

The effects of the RSD of artificial lighting on plant growth and leaf photosynthesis for enhancing productivity of horticultural facilities have been intensively investigated. Owing to the acclimation response, leaves grown under different RSDs of light are expected to represent a different RSD-dependency of the ETR and, thus, photosynthetic characteristics. Therefore, evaluating photosynthesis of leaves grown under different RSDs of light using an identical RSD of light might result in a biased evaluation. Although this possible bias was pointed out (e.g. Walters 2005), its significance on photosynthetic evaluation has not yet been experimentally demonstrated considering the horticultural situations. Therefore, quantitative analyses of the RSD-dependency of the ETR are essential for a comprehensive understanding of the light acclimation responses of a leaf and the evaluation of leaf photosynthesis toward efficient light use in horticultural plant production systems. The objective of this dissertation was to analyze the adjustments of the distribution of EE between the photosystems in response to the RSD of light and its influence on the ETR. In chapter 2, a novel method for estimating the EE distributed to PSII is proposed. In chapter 3, the electron transport based on the distribution of EE is illustrated as a mathematical model. Chapter 4 demonstrates that the acclimation response under different RSDs of growth light biased the evaluation of the net photosynthetic rate (P_n) in a practical horticultural situation.

Chapter 2. Quantification of excitation energy distribution between photosystems based on a mechanistic model of photosynthetic electron transport

The fraction of the EE distributed to PSII (*f*) depends on the wavelength of light (e.g. Evans 1986). The SD of *f* appears to be adjusted by at least two mechanisms in response to the RSD of light on different timescales (e.g. Dietzel et al. 2008); the adjustment of the photosystem stoichiometry (long-term response) and reversible reallocation of the light-harvesting complex between the photosystems (state transitions; short- term response). A quantitative evaluation of the EE distributed to the photosystems is required to comprehend the functioning and physiological roles of these mechanisms in the acclimation of the photosynthesis to the light environment.

In this chapter, a non-destructive, quantitative, and mechanistic method for estimating the *in vivo* *f* values of a leaf was developed and validated. To estimate the *f* values, a mechanistic model, which illustrates the ratio of photochemical quantum yields of PSII and PSI (Y_{II} and Y_I) from the *f* values and photon flux densities (PFDs) of the two simultaneously provided RSDs of actinic lights (ALs), was developed. This model assumes that the EE from individual ALs is distributed additively to the respective photosystems and that the ETRs through PSII and PSI are equal. By fitting values of Y_{II} and Y_I, obtained by monitoring chlorophyll fluorescence and leaf reflectance, under ALs provided at several PFD combinations into the model using the least-squares (i.e. curve-fitting) method, *f* values for the ALs can be estimated. This method was tested by comparing *f* values for red and far-red LED lights (R and FR, respectively) of cucumber leaves presumably giving different *f* values owing to the long- and short-term responses. The leaves were grown under white LED light (W; 300 μmol m^{-2} s^{-1}) with and without supplemental FR (100 μmol m^{-2} s^{-1}) for about 1 week to induce the long-term response. They were then pre-irradiated with R with and without supplemental FR for about 10 min to induce the short-term response, and then subjected to the *f* estimation. Irrespective of conditions of the long- and short-term responses, the quantified *f* values for R were clearly greater than those for FR. The values of the leaves subjected to 1-week supplemental FR (i.e. grown under W+FR) tended to be greater than those of the control (i.e. grown under W), presumably due to the long-term response. The values of the leaves subjected to 10-min of supplemental FR (i.e. pre-irradiated with R+FR) tended to be greater than those of the control (i.e. pre-irradiated with R), presumably due to the short-term response. These trends are consistent with those of earlier studies on the wavelength dependency of the *f* (e.g. Evans 1986), long-term response (e.g. Chow et al. 1990), and short-term response (e.g. Allen 1983). Furthermore, the fitted curve generated by the model was in agreement with the actual values in all experiments, supporting the validity of the model.

Chapter 3. A mathematical model of photosynthetic electron transport based on excitation energy distributed to photosystems for estimation of the electron transport rate

Simultaneously provided PSII- and PSI-light (light under which the whole-chain ETR is limited by photochemical reactions in PSII and PSI, respectively) produce a greater gross photosynthetic rate (P_g) than the sum of P_g under PSII-light and that under PSI-light (e.g. Emerson et al. 1957). This phenomenon, called the 'enhancement effect', led to the idea that electron transport occurs in series through the photosystems (Hill and Bendall 1960). It is generally accepted that the distribution of EE between the photosystems determines the photosynthetic quantum yield (e.g. Evans 1986). However, the electron transport in response to the EE distribution has not yet been illustrated as a mathematical model. Several available methods estimate the EE distribution from the SD of light (e.g. Evans 1986 and Chapter 2); therefore, developing a model may enable the estimation of the ETR in response to the SD of light.

In this chapter, a mathematical model, which illustrates the photosynthetic electron transport based on the EE distributed to the photosystems, was developed. This model assumes that 1) the whole-chain ETR is given as the minimum of potential ETR at either PSII or PSI, 2) the rate-limiting photosystem represents potential ETR by maintaining its maximum photochemical quantum yield, and 3) the photochemical quantum yield of the non-rate-limiting photosystem is passively down-regulated to equalize the actual ETRs through the two photosystems. To test the proposed model, Y_{II}, Y_I, and ETR of cucumber leaves under simultaneously provided R and FR were estimated from the EE distributed to the photosystems, which was calculated as described in Chapter 2, and compared to the actual values. Because the actual ETR could not be assessed directly, the estimated ETR was converted into P_g and compared to the actual P_g. The estimated values of Y_{II}, Y_I and P_g based on the model were in agreement with the actual values. The model explained the mechanisms determining the quantum yield of photosynthetic electron transport under light-limited conditions reasonably well.

Chapter 4. Interaction between the spectral photon flux density distributions of light during growth and for measurements in net photosynthetic rates

The P_n is often measured, compared, and evaluated among leaves of plants grown under different RSDs of light. Leaves adjust the distribution of EE in response to the RSD of growth light (GL) (e.g. Anderson 1986). Therefore, even when evaluated under light with the same RSD, the EE distributed to the respective photosystems will be modified depending on the RSD of GL. That is, the RSDs of GL and AL interact on the ETR and thus P_n through the EE distribution. When the effect of the interaction is considerable, the P_n of leaves compared using a single RSD of AL does not always reflect their relationship under other RSDs of light. Although some earlier physiological studies have already demonstrated the significance of this interaction (Chow et al. 1990, Walters and Horton 1995, Hogewoning et al. 2012), it has not yet been clarified that the interaction should be considered even in practical situations.

This chapter describes how the significance of the interaction was examined in a practical situation imitating seedling production. The effects of the RSD on seedling growth and photosynthetic characteristics have been intensively investigated (e.g. Shibuya et al. 2015). As the seedlings are grown under artificial light sources and then under sunlight, the photosynthesis under both conditions should be discussed. However, most of recent measurements of P_n were made using blue and red LED light (BR) preinstalled in widely- used instruments. P_n of leaves of cucumber seedlings grown under W (300 μmol m^{-2} s^{-1}) with and without supplemental FR (70 μmol m^{-2} s^{-1}) were measured and compared under three different RSDs of ALs: their respective GL, BR, and light with a RSD approximate to that of sunlight (artificial sunlight; AS). The P_n of W+FR-grown-leaves was lower than that of W-grown-leaves under BR, moderate PFD (300 μmol m^{-2} s^{-1} within 400–700 nm), and ambient CO_2 (40 Pa) conditions, whereas no significant difference was found between the leaves under GL and AS under the same PFD and CO_2 conditions. In short, the RSDs of GL and AL interacted on the P_n. Analyses of the photochemical yields of photosystems showed that the interactions in P_n were related, at least partly, to the distribution of EE. It was demonstrated that the evaluation of P_n of leaves grown under different RSDs of light could be biased depending on the RSD of AL even in practical situations. P_n should be discussed in connection to the RSD of AL especially when leaves of plants grown under different RSDs of GL are compared.

Chapter 5. Conclusions

This dissertation focused on the distribution of EE between PSII and PSI in response to the RSD of light and its influence on photosynthetic electron transport. A non-destructive and quantitative method for estimating *in vivo* distribution of EE was developed. The f estimation was performed based on a mechanistic model of electron transport, in which the EE distributed to respective photosystems are additive and the ETRs through PSII and PSI are equal. The contributions of mechanisms adjusting the distribution were compared based on an identical quantitative measure, i.e. the fraction of EE distributed to PSII or the f value. In addition, by assuming that the rate-limiting photosystem represents its maximum efficiency, the electron transport under light-limited conditions was illustrated as a mathematical model based on the distribution of EE. The interaction between the RSDs of light for measurement and during growth on leaf P_n was shown to be significant even in practical situations. The necessity of a circumspect consideration of the distribution of EE between the photosystems in evaluating leaf photosynthesis was emphasized.