Photosynthetic Light Reactions in C_4 Photosynthesis

Naoya Nakamura[a], Yuri Nakajima Munekage[a], Akiho Yokota[a*]

[a]*Graduate School of Biological Sciences, Nara Institute of Science and Technology*
** Corresponding author: Graduate School of Biological Sciences, Nara Institute of Science and Technology, 8916-5 Takayama, Ikoma, Nara, 630-0192 Japan*
Tel.: +81 0743 72 5568; fax: +81 0743 72 5569.
yokota@bs.naist.jp

Abstract

The most productive wild plants and crops use C_4 photosynthesis (Brown, 1999). C_4 photosynthesis requires the coordinated functions of two cell types in leaves, namely mesophyll (M) - and bundle-sheath (BS) - cells (Hatch, 1987). Atmospheric CO_2 is initially fixed by phosphoenolpyruvate carboxylase (PEPC) in M cells. The resulting products, C_4 acids are transported into BS cells where CO_2 is released by decarboxylation of C_4 acids and refixed by riburose-1, 5-bisphosphate carboxylase/oxygenase (RuBisCO) functioning in the Calvin cycle (C_3 cycle). Since this process increase CO_2 levels at the site of RuBisCO in the BS cells, the oxygenase reaction of RuBisCO is largely reduced and RuBisCO can achieve maximal catalytic activity of CO_2 fixation. Therefore, C_4 plants have higher potential efficiencies in the use of light, water and nitrogen than C_3 plants (Long, 1999). C_4 plants have evolved from ancestral C_3 plants (Sage *et al.*, 2011). In C_4 plants, not only the CO_2 metabolism but a manner of light reactions which is a process to produce ATP and NADPH used for CO_2 metabolism has been changed. However, mechanism of light reactions and its physiological roles on C_4 photosynthesis are not yet fully understood. Here, we introduce latest findings and perspectives of physiological roles of light reactions in C_4 photosynthesis.

Keywords: C_4 photosynthesis, cyclic electron flow, Flaveria, Zea mays

The structure of mesophyll and bundle-sheath chloroplasts: the regulation of grana formation

Light reactions take place on thlakoid membranes in chloroplasts. The thylakoid membranes are arranged in stacked (grana) and unstacked (stroma lamellae) in C_3 plants. Supercomplex of photosystem (PS) II and light-harvesting complex of photosystem II (LHC-II) are localized in grana thykoids while most of PSI and ATP synthase are localized in stroma lamellae (Albertsson, 2001). The grana stacks are more developed in low light intensity than in high light intensity, the changes are assumed to optimize the photosynthetic efficiency in C_3 plants (Ballantine and Forde, 1970). In NADP-malic enzyme (ME) type C_4 plants such as *Zea mays*, *Sorghum bicolor* and *Flaveria trinervia*, grana thylakoids are observed in the M chloroplasts like chloroplasts of C_3 plants, but BS cells possess chloroplasts where grana thylakoids are largely decreased, as shown in Fig. 1 (Laetsch *et al.*, 1965, Laetsch and Price, 1969, Hofer *et al.*, 1992). Interestingly, grana formation was observed in BS chloroplasts of maize leaves at very low light intensity but was completely abolished at normal light intensity (Brangeon, 1973). Decrease in grana stacks of BS chloroplasts is likely induced by high light signal and those systems would have been recruited from C_3 plants during C_4 evolution.

LHC-II is suggested to be involved in grana formation by binding thylakoid membranes in C_3 plants (Allen and Forsberg, 2001, Standfuss *et al.*, 2005). LHC-II is mainly present as trimer on grana thylakoids. It is reported that in *Flaveria trinervia* the amounts of LHC-II polypeptides in BS chloroplasts is only slightly reduced compared with that in M chloroplasts (Hofer *et al.*, 1992) and a significant amount of LHC-II polypeptides are also detected in fractionated stroma lamellae (Munekage *et al.*, 2010). Moreover, in maize, LHC-II trimer is identified in BS thylakoid membranes

using Blue-Native PAGE, although BS chloroplasts of Maize are almost grana-free (Romanowska *et al.*, 2008). These results suggest that amounts of LHC-II polypeptide and the presence of LHC-II trimer are not sufficient for grana formation. Perhaps the additional mechanism is involved in the formation of thylakoid membranes with reduced grana in BS chloroplasts.

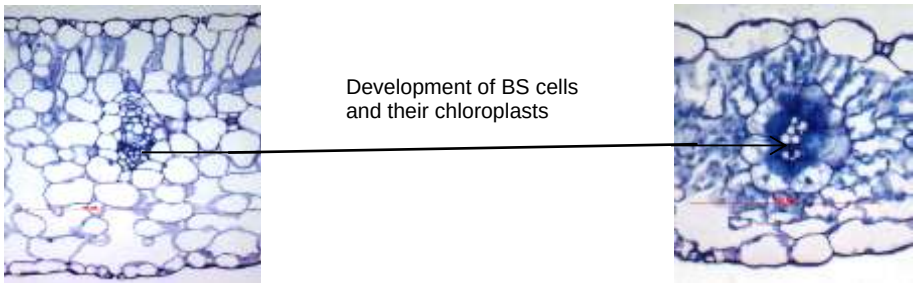

Figure 1. Light micrograph's of leaf transverse section of *Flaveria species.*

Regulation of linear electron flow and cyclic electron flow around PSI in C_4 photosynthesis

Linear electron flow operates to produce the both ATP and NADPH. In linear electron flow, the electrons excised from water molecules at PSII are transferred to PSI through the cytchrome b_6f complex, and finally NADPH is produced. Protons are transported across the thylakoid membranes from stroma side to lumen side during the process of electron transfer. This proton gradient is used for ATP synthesis (Fig. 2). On the other hand, cyclic electron flow around PSI (CEF1) contributes to only ATP production. In CEF1, electrons are returned from accepter side of PSI to plastoquinone which mediate electron transport from PSII to cytchrome b_6f complex (Shikanai, 2007). This electron transport contributes to form proton gradient without NADPH production. Two CEF1 pathways have been identified in C_3 plants.

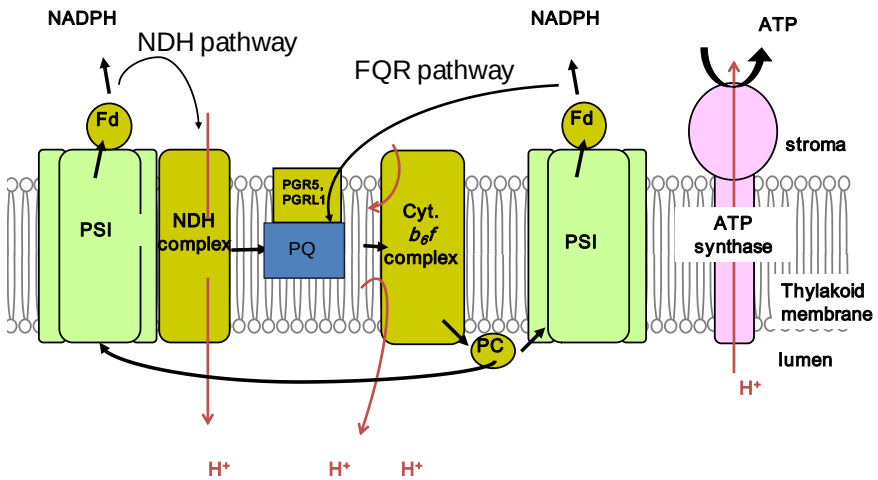

Figure 2. Schematic model of PS1 cyclic electron transport.

The first pathway is called as ferredoxin-plastoquinone reductase (FQR) pathway involving PROTON GRADIENT REGULATION 5 (PGR5) and PGRL1 (Munekage *et al.*, 2002, Dalcorso *et al.*, 2008). The other pathway is NAD(P)H dehydrogenase (NDH) pathway involving a plastidial NDH

complex composed of the eleven plastid-coded subunits (NDH-A to -K) and the over 15 nuclei-encoded subunits (Peng *et al.*, 2011). In C_3 plants, the FQR pathway contributes for maintaining the production ratio of ATP/NADPH and for photoprotection, whereas the NDH pathway functions in stress resistance in C_3 plants (Munekage *et al.*, 2004, Wang *et al.*, 2006, Munekage *et al.*, 2008). Localization of the NDH complex and PGR5 on stroma lamellae and distribution of PSII and PSI on thylakoid membrane suggest that CEF1 takes place in stroma lamellae (Rumeau *et al.*, 2005, Munekage *et al.*, 2010).

In C_4 plants, increased CEF1 activity and decreased linear electron transport is induced. In NADP-ME type C_4 plants, BS chloroplasts of mature leaves show the inhibition of PSII activity (Woo *et al.*, 1970). The composition of PSII complex in BS chloroplasts is investigated by many researchers using *Zea mays*, *Sorghum bicolor* and *Flaveria trinervia*. Several studies are suggested that the subunits of PSII complex, especially those of oxygen evolving complex are largely reduced in BS chloroplasts compared with M chloroplasts (Sheen *et al.*, 1987, Oswald *et al.*, 1990, Hofer *et al.*, 1992). BS chloroplasts produce only limited amounts of ATP and NADPH from liner electron flow activity, because in this chloroplasts, PSII activity is significantly inhibited (Schuster *et al.*, 1985). Since NADPH is supplied by decarboxylation of C_4 acids by NADP-ME, only ATP is required to be produced in BS chloroplasts of NADP-ME type. The ATPs are considered to be produced by CEF1 activity. Significant activity of CEF1 compared with C_3 plants has been reported in *Zea mays*, *Sorghum bicolor* (Herbert *et al.*, 1990, Asada *et al.*, 1993). The higher amounts of NDH complex and PGR5 in BS cell than M cell also supports activation of CEF1 in BS cell of NADP-ME type C_4 plants (Kubicki *et al.*, 1996, Munekage *et al.*, 2010). On the other hand, ATP demands are increased in M chloroplasts in NAD-ME type C_4 metabolism. In *Salsola laricina* and *Halocharis gossypina* carrying NAD-ME type C_4 photosynthesis, lower grana index and higher ratio of PSI/PSII in M chloroplasts than BS chloroplasts are reported (Voznesenskaya *et al.*, 1999). Moreover, subunits of NDH complex are enriched in M chloroplasts of NAD-ME type C_4 plants (Takabayashi *et al.*, 2005). Activated CEF1 likely contributes to the ATP production in C_4 photosynthesis. However, for final conclusion, it is need to investigate phenotype of transgenic plants in which genes involved in CEF1 are knocked down.

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