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Review

Molecular mechanisms of RuBisCO biosynthesis in higher plants

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Abstract Ribulose 1,5-bisphosphate carboxylase/oxygenase (RuBisCO) catalyses the initial step of photosynthetic CO_2 assimilation, although its catalytic efficiency is very low. Therefore, higher plants must synthesize large amounts of RuBisCO to compensate for its inefficient enzymatic properties. The holoenzyme of RuBisCO consists of 8 large and 8 small subunits, whose genes are individually encoded on two distinct genomes located in the chloroplast and the nucleus, respectively. RuBisCO biosynthesis requires many factors involved in transcription, translation, folding and assembly processes. However, the mechanisms underlying these processes are complex, and therefore the molecular mechanisms and regulation systems of RuBisCO biosynthesis are not yet fully understood. In this review, we introduce recent research on the molecular mechanisms of RuBisCO biosynthesis in higher plants, and discuss future perspectives in this field of research.

Key words: Chloroplast, photosynthesis, protein biosynthesis, RuBisCO.

RuBisCO is a key enzyme catalyzing the CO_2-fixing reaction in the initial step of the Calvin cycle. However, its enzymatic properties are inadequate for plants because of its small turnover rate of the carboxylase reaction (Harris and Koniger 1997) and its low affinity for CO_2. Thus, this enzyme limits the rate of carbon assimilation and net photosynthesis (Yokota and Shigeoka 2007). To compensate for its enzymatic inefficiencies, RuBisCO comprises as much as half of leaf total soluble proteins in higher plants, corresponding to 30% of total nitrogen compounds in the leaves. Consequently RuBisCO is regarded as the most abundant protein in the world (Gatenby and Ellis 1990; Makino et al. 2003). Indeed, a decrease in the amount of RuBisCO causes strong inhibition of CO_2 assimilation and subsequent growth retardation (Rodermel et al. 1988; Quick et al. 1991; Hudson et al. 1992; Masle et al. 1993). Therefore, it is important to understand how plants synthesize RuBisCO abundantly and maintain a sufficient amount for growth and development. How is RuBisCO synthesized optimally in plant chloroplasts?

Gene expression of nuclear- and chloroplast-encoded subunits of RuBisCO

RuBisCO functions as an enzyme in the chloroplast stroma with a hexadecameric structure consisting of eight large (LSU) and eight small subunits (SSU). LSUs and SSUs are synthesized through distinct processes as the genes encoding them are individually located on different genomes (Figure 1). SSU is encoded by *rbc*S in the nuclear genome as a multigene family ranging from 2 to 12 members (Gutteridge and Gatenby 1995). The expression of *rbc*S is regulated by various endogenous and/or exogenous signals, such as light/dark transition, light quality, circadian rhythm, temperature, atmospheric CO_2 concentration, and nitrogen supply. It is also controlled in an organ- and tissue-specific manner, and by developmental stages (Sugita and Gruissem 1987; Dedondar et al. 1993; Pilgrim and McClung 1993; Gesch et al. 1998; Yoon et al. 2001; Imai et al. 2007). The relationship between *rbc*S expression and light conditions has been studied well. The signal transduction pathway mediated by phytochrome and the G protein is involved in light-stimulated transcription and light quality-dependent expression pattern of *rbc*S (Zhou 1999). Dark-induced down-regulation of *rbc*S expression is regulated by CONSTITUTIVELY MORPHOGENIC/DE-ETHIOLATED/FUSCA (COP/DET/FUS), which are well known as repressors of photomorphogenesis (Millar et al. 1994). However, *cis* elements or *trans*-acting factors involved in the regulation of the *rbc*S expression response to various endogenous and/or exogenous signals are not well understood.

After transcription in the nucleus, *rbc*S mRNA is translated on 80S ribosomes in the cytosol to synthesize the precursor protein of SSU (PreSSU) with the transit peptide in its *N*-terminal required for targeting to the chloroplast. The PreSSU is carried to the chloroplast outer membrane by heat shock protein70 (hsp70) and 14-

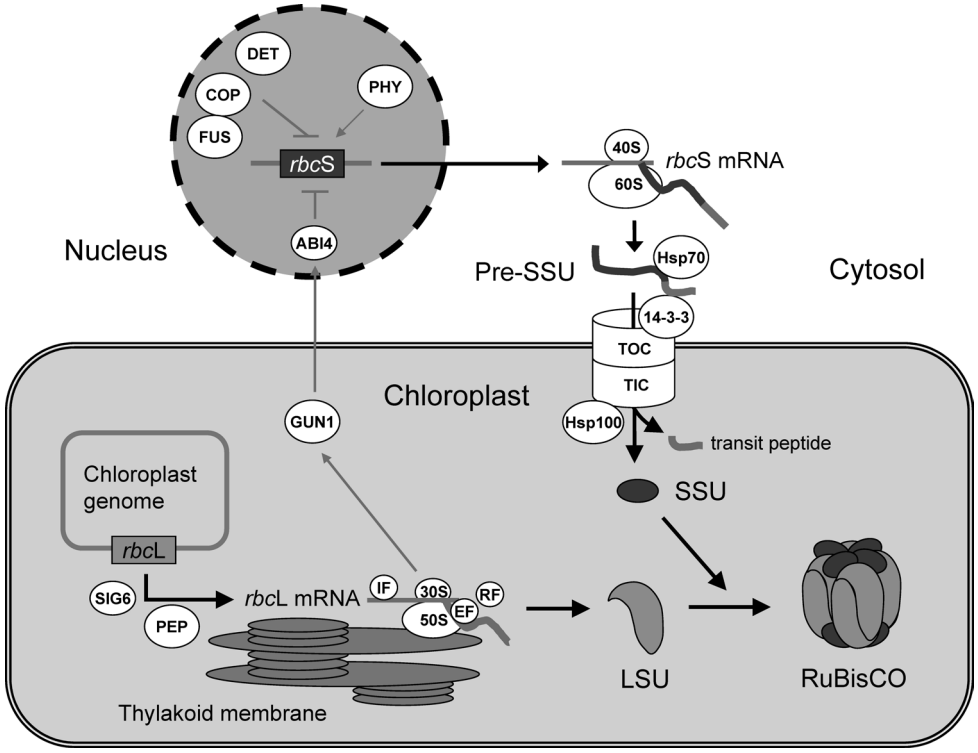

Figure 1. RuBisCO biosynthesis in higher plants. Arrows indicate steps of RuBisCO biosynthesis; transcription, translation, import of pre-SSU, folding and assembly. Circles show factors involved in steps of RuBisCO biosynthesis before folding and assembly (folding and assembly steps shown in Figure 2). Large and small subunits of RuBisCO are synthesized in distinct subcellular compartments, but both syntheses are coordinately regulated. Transcription of *rbc*S is positively regulated by PHY (grey arrows). Translation of *rbc*L mRNA in chloroplasts is coupled with transcription of *rbc*S in the nucleus via the signaling pathway mediated by GUN1 and ABI4. COP, DET and FUS are negative regulators for transcription of *rbc*S (grey T-shaped line). *Abbreviations*: ABI4, ABSCISIC ACID-INSENSITIVE4; COP, CONSTITUTIVELY PHOTOMORPHOGENIC; DET, DE-ETHIOLATED; FUS, FUSCA; EF, Prokaryotic-like elongation factor; GUN1, GENOME UNCOUPLED1; Hsp, Heat shock protein; IF, Prokaryotic-like initiation factor; PEP, Plastid-encoded plastid RNA polymerase; PHY, phytochrome; Pre-SSU, Precursor of SSU; RF, Prokaryotic-like release factor; SIG, sigma-like factor; TIC/TOC, Translocons at the inner and outer envelope membranes of chloroplasts, respectively.

3-3 protein as the guidance complex, and then imported into the chloroplast stroma via translocons located within the outer and inner envelope membranes of chloroplasts (Toc and Tic complexes, respectively) (Jarvis and Soll 2001; Soll 2002). The transit peptide of preSSU is cleaved by the stromal processing peptidase (SPP) and the mature SSU is produced (Jarvis and Soll 2001).

LSU is encoded by *rbc*L, which is located on the chloroplast genome. This gene is transcribed by the plastid-encoded plastid RNA polymerase (PEP) which functions in the expression of the other genes related to photosynthesis. The specificity for target genes and the spatial-temporal regulation of PEP-mediated transcription are regulated by nuclear-encoded sigma-like transcription factors (SIGs) (Isono et al. 1997; Kanamaru and Tanaka 2004; Tsunoyama et al. 2004; Favory et al. 2005; Loschelder et al. 2006; Tozawa et al. 2007; Zghidi et al. 2007). AtSIG6, which is one of the six SIGs identified in *Arabidopsis*, is involved in *rbc*L gene expression during the early developmental stage when the biosynthesis of RuBisCO is most active (Ishigaki et al. 2005).

*rbc*L mRNA is translated on prokaryotic-type 70S ribosomes with prokaryotic translation apparatus, such as initiation factors, elongation factors and termination factors (Murayama et al. 1993; Millen et al. 2001; Motohashi et al. 2007). Interestingly, it is suggested that LSU is translated on the membrane-bound ribosomes, as well as chloroplast-encoded thylakoid membrane proteins (Mühlbauer and Eichacker 1999). The translation of *rbc*L mRNA is enhanced by light via activation of the translation elongation process (Mühlbauer and Eichacker 1999). It has been proposed that this light-induced enhancement of the translation elongation of LSU on thylakoid-bound polysomes is mediated by the proton gradient formed across the thylakoid membranes (Mühlbauer and Eichacker 1998; Mühlbauer and Eichacker 1999). In addition, the specific activity of the elongation factor EF-G and the expression of EF-Tu are enhanced by light, and these are also suggested to contribute to the light-induced enhancement of the translation elongation of *rbc*L (Akkaya and Breitenberger 1992; Singh et al. 2004; Marin-Navarro et al. 2007).

The genes encoding LSU and SSU are separately located in the different subcellular compartments, but the

synthesis of each subunit of RuBisCO proceeds under fine controls to ensure that there are no free subunits in the stroma. In fact, in transgenic tobacco plants expressing antisense RNA for *rbc*S, the translation initiation of *rbc*L mRNA was disturbed concomitantly, resulting in a decreased amount of the RuBisCO holoenzyme (Rodermel et al. 1988; Rodermel et al. 1996). This fact indicates that the SSU imported into chloroplasts acts as a positive regulator of the *rbc*L translation initiation directly or indirectly; however the mechanism by which this occurs is still unknown (Rodermel 1999). Likewise, it is known well that the reduction of *rbc*S expression results from inhibition of chloroplast translation by chloramphenicol or lincomycin (Nott et al. 2007). Recent genetic studies showed that GENOME UNCOUPLED1 (GUN1), a member of the pentatricopeptide repeat protein family, and an APETALA2-type transcription factor ABSCISIC ACID-INSENSITIVE4 (ABI4) play key roles in the signaling pathway underlying the coordinated regulation between the translation in the chloroplast and gene expression in the nucleus (Koussevitzky et al. 2007; Zhang 2007). Furthermore, these two regulatory events imply that *rbc*S transcription and the *rbc*L translation are the key steps in controlling RuBisCO biosynthesis. Thus, the syntheses of SSU and LSU are optimally regulated via intracellular crosstalk between the nucleus and the chloroplast.

Folding and assembly into the RuBisCO holoenzyme in chloroplasts

The processes of folding and assembly of RuBisCO in higher plants are shown in Figure 2. Newly synthesized LSU forms a multimeric complex with several chloroplast molecular chaperones. Likewise, SSU is also associated with the chloroplast chaperones after cleavage of a transit peptide (Gutteridge and Gatenby 1995). These chaperones promote protein folding of each subunit and assembly of RuBisCO's LSUs and SSUs (Houtz and Portis 2003). LSU is assembled with SSU after dissociation from the chaperone complex to construct a holoenzyme, but the process remains to be revealed in higher plants. The model for assembly of LSU and SSU has been proposed in cyanobacteria; in this model, LSU_8SSU_8 is formed through the octameric LSU intermediate (LSU_8 core), and the LSU_8 core and SSUs assemble to form LSU_8SSU_8 (Golouginoff et al. 1989). A LSU_8 core-like particle has been detected in an *in vitro* assay using isolated intact chloroplasts under relatively high ionic strength conditions (Hubbs and Roy

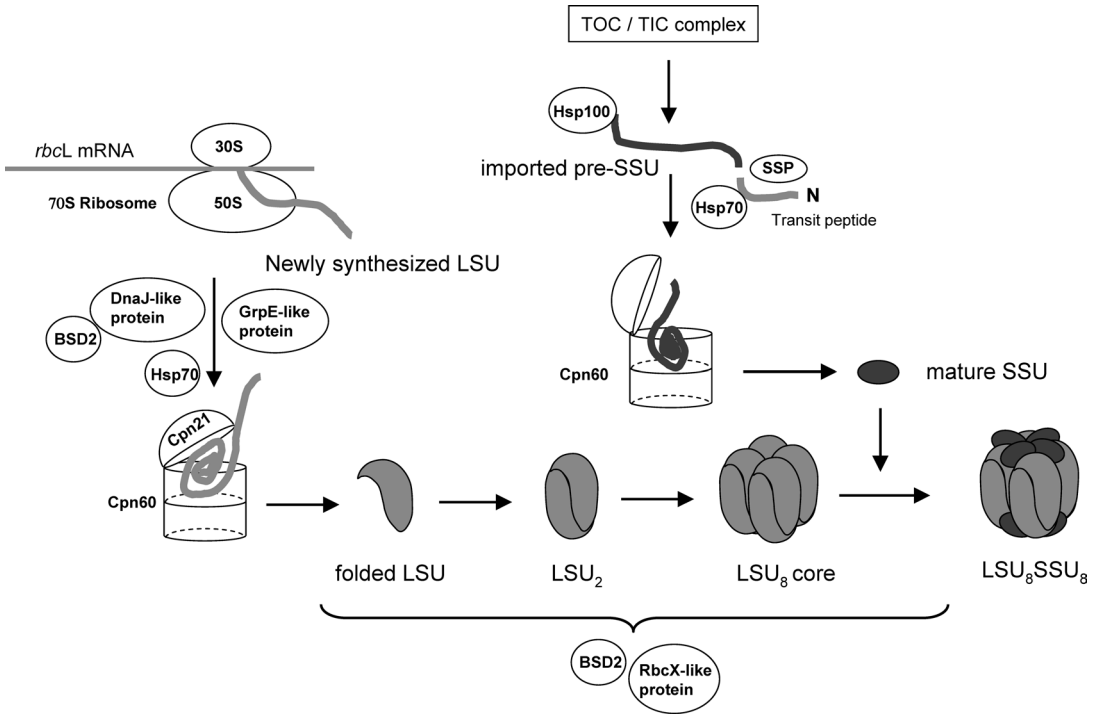

Figure 2. Schematic model for folding and assembly of LSU and SSU into the RuBisCO holoenzyme in chloroplasts. Schematic model is fundamentally based on reports of Brutnell et al. (1999), Roy (1989) and Saschenbrecker et al. (2007). Newly synthesized LSU is folded through the chaperone systems containing DnaJ-, DnaK (Hsp70)-, and GrpE-like proteins and the cpn60/cpn21 complex. BSD2 may be also involved in this process. After import into chloroplasts and processing of the transit peptide by SPP, SSU is folded by cpn60 possibly cooperating with Hsp100 and Hsp70. After release from the Cpn60/Cpn21 complex, the folded monomer of LSU may be assembled to intermediate dimeric (LSU_2) and octameric structures (LSU_8 core) as observed in cyanobacteria. In the final step, the LSU_8 core and SSUs assemble. BSD2, RbcX-like proteins and other unknown factors may be involved in the assembly process. *Abbreviations*: BSD2, BUNDLE SHEATH DEFECTIVE2; Cpn, chaperonins; SPP, Stromal processing peptidase.

1993). Therefore, it is predicted that the assembly of RuBisCO in higher plants may follow a similar assembly process to that of cyanobacteria.

It was proposed that a bacterial-type chaperone system was involved in the process of folding and assembly into LSU_8SSU_8 (Brutnell et al. 1999; Jarvis and Soll 2001; Houtz and Portis 2003; Kessler and Schnell 2006). Indeed, homologs of DnaJ/DnaK/GrpE possess putative chloroplast-targeted sequences (Wang et al. 1993; Brutnell et al. 1999). Chaperonin60 (cpn60) and its co-factor, chaperonin21 (cpn21) of chloroplasts correspond to GroEL and GroES in *Escherichia coli*, respectively. Cpn10 is also known as a co-chaperonin of cpn60. However, it is suggested that cpn10 and cpn21 work independently because the gene expression and protein accumulation pattern of these two chaperonins differ from each other (Koumoto et al. 2001). We need further studies to elucidate a functional relationship between these two chaperonins. Although cpn60 was first isolated as a RuBisCO-binding protein, it also interacts with a wide range of chloroplast proteins (Lubben et al. 1993). The cotyledon-specific chloroplast maturation factor CYO1 is a chaperone-like protein that possesses protein disulphide isomerase activity and a C4-type zinc finger domain essential for DnaJ function. These attributes suggest that this chaperone-like protein is required for the folding of multiple chloroplast proteins in *Arabidopsis* (Shimada et al. 2007). On the other hand, maize BUNDLE SHEATH DEFECTIVE2 (BSD2) is suggested to be the only factor that is specific for folding and assembly of RuBisCO (Brutnell et al. 1999). BSD2 is localized in the chloroplast and possesses a cysteine-rich Zn-binding domain that is thought to play a key role in the protein-protein interaction in DnaJ. Therefore, it is speculated that BSD2 may function in LSU folding or assembly of the holoenzyme by direct interaction with the LSU polypeptide or via binding with other chaperone-related proteins. C3 plants, such as tobacco and *Arabidopsis*, also possess homologous genes to maize BSD2, it is suggested that the tobacco homolog may function in a similar manner as observed in maize (Wostrikoff and Stern 2007). However, the actual biosynthesis step of RuBisCO mediated by BSD2 is still unknown.

Although research on the specific factors for RuBisCO assembly has been underway for a long time, they are yet to be identified in higher plants. Recently, it was shown that RbcX is a specific assembly chaperone of the hexadecameric RuBisCO holoenzyme in *Synechococcus* sp. PCC7002 (Onizuka et al. 2004; Saschenbrecker et al. 2007). The RbcX directly binds to the C-terminal polypeptide of LSU to stabilize the LSU_8 core structure and protect it from aggregation. RbcXs bound to the LSU_8 core are subsequently displaced by SSUs to form the LSU_8SSU_8 RuBisCO (Saschenbrecker et al. 2007). Interestingly, two homologous genes of cyanobacterial *rbc*X can be found in the *Arabidopsis* genome and the RbcX recognition polypeptide is also conserved in higher plants' C-terminal of the LSU sequence. These RbcX homologs are also expected to be involved in RuBisCO assembly in plants.

Many factors required for assembly of the photosynthetic supercomplexes located within the chloroplast thylakoid membranes have been identified in recent years. It should be noted that some of these factors include immunophilin family proteins. Immunophilins were originally discovered in animals as receptors for immunorecessive drugs and are classified into two subgroups; cyclophilins (CYPs) and FK506-binding proteins (FKBPs). It is thought that immunophilins are protein foldases or chaperones with peptidyl prolyl isomerase activity. Interestingly, they are also present as large protein families in higher plants, 5 CYPs and 11 FKBPs are located in the chloroplast lumen (He et al. 2004; Romano et al. 2004). In *Arabidopsis*, it is suggested that CYP38 is involved in the assembly of photosystem II (PSII) and FKBP20-2 is an essential factor for maintenance of the PSII complex (He et al. 2007; Lima et al. 2007), suggesting the possibility that one or several immunophilins may also be required for RuBisCO assembly (Houtz and Portis 2003). Indeed, several immunophilin proteins are observed or predicted to be in the chloroplast stroma (He et al. 2004). The relationship between the functions of these stromal immunophilins and the assembly of RuBisCO attracts our interest.

Conclusion and future perspective

Higher plants synthesize large amounts of RuBisCO, which comprises a substantial portion of leaf soluble proteins to compensate for its catalytic inefficiencies. The massive production of RuBisCO is essential for optimal photosynthesis and plant growth. To achieve this, there is a complex regulatory mechanism regulated by many factors. Nevertheless, many questions remain to be answered concerning the molecular mechanisms for RuBisCO biosynthesis. To address these questions, it is necessary to understand the molecular entities involved in RuBisCO biosynthesis. Because RuBisCO is a metabolically essential enzyme, plants defective in its biosynthesis will exhibit apparent phenotypes (Kanevski and Maliga 1994). In addition, the plant leaves contain this enzyme abundantly. Considering these features of RuBisCO, genetic and biochemical methods are suitable to analyze its biosynthesis. Therefore, comprehensive screening of mutant plants with decreased amounts of RuBisCO is an effective and fascinating approach to explore the molecular entities required for its synthesis. Using this approach, we may be able to isolate genes that are involved in RuBisCO biosynthesis.

As mentioned above, the RuBisCO holoenzyme is

composed of nuclear- and chloroplast-encoded subunits. Therefore, RuBisCO is a suitable model protein to understand the biogenesis of chloroplast proteins. Indeed, many processes of protein biosynthesis overlap between RuBisCO and other chloroplast proteins. Therefore, analysis of RuBisCO biosynthesis should provide beneficial information about biosynthesis of various chloroplast proteins.

In recent years, chloroplasts have attracted attention as a place to synthesize large amounts of foreign proteins because of their high potential for protein synthesis, as in the case of RuBisCO. Since chloroplast transformation was established, there have been some reports on production of biopharmaceuticals in the chloroplasts of plant leaves. More effective production of these biopharmaceuticals will be achieved using information of chloroplast protein biosynthesis that results from analysis of the molecular mechanisms of RuBisCO biosynthesis.

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