Hypothesis

Translational regulation of plastid gene expression in *Euglena gracilis**

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Translation of plastid messenger RNAs depends on aminoacyl-tRNAs formed by charging plastid-encoded tRNAs with cognate amino acids. The enzymes involved, chloroplast aminoacyl-tRNA synthetases, are encoded in the nucleus. Both the tRNAs and the aminoacyl-tRNA synthetases are stimulated in synthesis if dark-grown cells are exposed to light. However, their accumulation during light-induced chloroplast development in *Euglena gracilis* starts with an appreciable lag-phase. During this period the availability of charged tRNAs probably limits protein synthesis. Due to the contemporary need of glutamyl-tRNA$^{Glu}_{GAA}$ in chlorophyll synthesis this particular tRNA is very likely depleted. Based on an analysis of glutamate codon frequency in known plastid genes, the effect of a glutamyl-tRNA$^{Glu}_{GAA}$ limitation on the translation of plastid messages is discussed.

Plastid gene expression; Elongation of translation; Glutamyl-tRNA limitation; Glutamate codon frequency in protein genes; *Euglena gracilis*

1. INTRODUCTION

Chloroplast development in *Euglena gracilis*, a complex phenomenon that includes qualitative and quantitative changes in gene expression of the plastid and nuclear genomes, is not yet fully understood [1–3]. The whole process starts with the morphological and biochemical differentiation of small proplastids, which are characterized by a limited extent of structural organization. Only prothylakoids and the prolamellar body are observed. After light induction, thylakoids are formed and organized into lamellae and pyrenoids appear [4–6]. On the other hand, little is known of the interdependence and coordinated regulation of plastid and nuclear gene expression during light-induced chloroplast development [2]. Detailed analysis at the protein and RNA levels [7–12] merely revealed that nuclear and plastid genes for chloroplast proteins are differentially expressed during the transformation of proplastids to chloroplasts. Changes in other plastid constituents like galacto- or sulfolipids [13,69], chlorophylls [14,15] and carotenoids [16,17] emphasized the complexity of biochemical processes. They only reflect but do not explain how the expression of plastid and nuclear genes is coordinated.

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* Dedicated to Prof. Dr. H. Kleinkauf on the occasion of his 60th birthday

In this review we hypothesize a model of translational regulation of plastid gene expression in the early phases of chloroplast development in *Euglena gracilis* depending on the limited supply of specific plastid aminoacyl-tRNAs, the charging of which depends on the cytoplasmically synthesized and posttranslationally imported chloroplast aminoacyl-tRNA synthetases.

2. EXPERIMENTAL FINDINGS

2.1. *Expression of nuclear genes for plastid proteins*

Plastid proteins of cytoplasmic origin are involved in plastid gene expression (e.g. ribosomal proteins [18]; aminoacyl-tRNA synthetases [19,74]), electron transport (thylakoid membrane proteins, e.g. LHCP [20,21]) and carbon dioxide fixation of photosynthesis (e.g. small subunits as part of RuBPCase holoenzyme [22]; NADP-dependent glyceraldehyde phosphate dehydrogenase [23]). They also participate in chlorophyll synthesis [24] and other intraplastidic pathways (e.g. synthesis of aromatic amino acids [25]).

The light-induced synthesis of most nuclear-encoded chloroplast proteins seems to be non-correlated with respective changes at the mRNA level. This post-transcriptional type of control was mainly deduced from identical patterns of in vitro translatable mRNAs [10–12,26,27] and was confirmed in a few cases with cloned gene probes [21]. In contrast to the vast majority certain nuclear-encoded plastid polypeptides are regulated at the transcription level [12,28]. Posttranslational transport of cytoplasmically synthesized proteins into *Euglena* chloroplasts probably occurs in situ, but

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this has been demonstrated in a homologous in vitro system only [27].

2.2. *Expression of plastid genes*

In spite of its limited capacity plastid DNA codes for several chloroplast constituents ([35–37] for reviews). In *Euglena* the genes for the following plastid constituents have been found encoded in plastid DNA: ribosomal RNAs [35], tRNAs [39], coding sequences for thylakoid [40–47] and stroma proteins, the latter either forming part of the gene expression apparatus, e.g. ribosomal proteins [48–50], subunits of the soluble RNA-polymerase [51], elongation factor Tu [52], or participating in carbon dioxide fixation, e.g. large subunits of RuBPCase [53,54]. These gene products are formed by transcription [55–57] and posttranscriptional reactions including steps of RNA maturation which are not yet characterized [42,44,47,58–61] and – for protein coding sequences – translation [26,62]. Plastid genes differ with respect to expression level during light-induced chloroplast differentiation from proplastids.

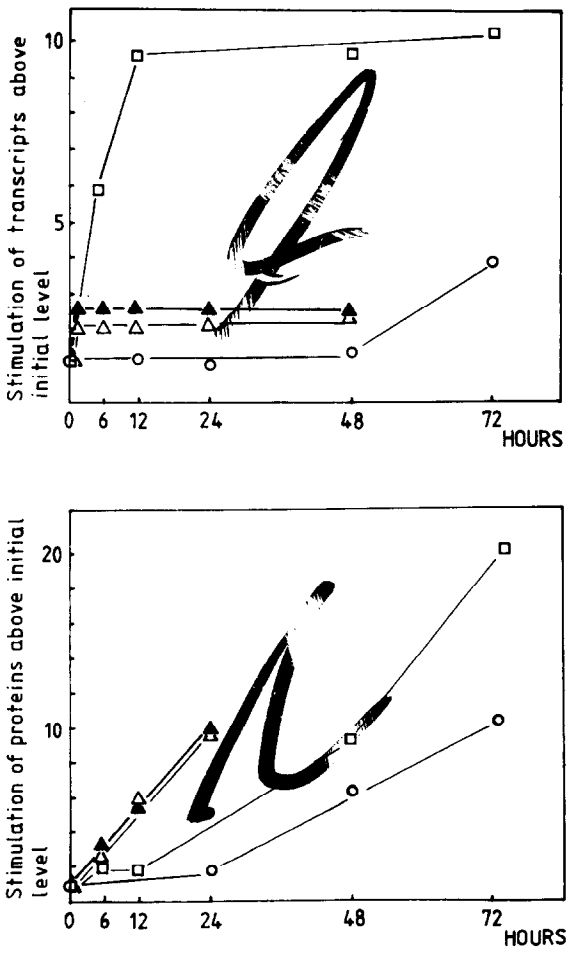

Fig. 1. Light-induced appearance of plastid transcripts and proteins in illuminated dark-grown *Euglena* cells. Symbols: (▲) psaA, (△) psbC, (○) tufA, (□) rbcL transcripts and respective polypeptides. Data taken from the literature [21,40,42,71,72] or representing our own unpublished results (for rbcL) are expressed as *n*-fold stimulation above initial level of dark-grown cells.

While certain genes are expressed constitutively [63–68], the expression of others is modulated by light [63–68]. At least two sets of gene products are discernible. Their transcript levels change in opposite directions upon illumination of dark-grown cells: (i) appearing transcripts; (ii) disappearing transcripts.

Transcripts of the first set either increase in amount continuously (e.g. for psbA [40]) or remain nearly constant after an initial rise in abundance (e.g. for psaA, psaB, psbC, psbD [21,42]; rbcL [40], and unpublished observations; cf. Fig. 1). The corresponding polypeptides are stroma polypeptides or thylakoid membrane proteins of the light-harvesting complexes called photosynthetic reaction centers. Most thylakoid proteins are synthesized and accumulated immediately upon illumination ([21,42]; cf. Fig. 1). They assemble with pigments [14–17], galacto- and sulfolipids [13,69] and other plastid- or nuclear-encoded polypeptides. Posttranslational import from the cytoplasm is required for the latter [20,21]. By integration into thylakoids they are protected from degradation. Stroma proteins like large subunits of RuBPCase, however, appear with an appreciable lag-phase, although the level of the rbcL transcript remains almost unchanged after an initial 'burst' of an at least 10-fold increase (Fig. 1). These data suggest that in addition to transcriptional control other not yet identified mechanisms regulate synthesis and accumulation of the plastid encoded proteins, temporally and spatially.

3. REGULATION OF PLASTID TRANSLATION (ELONGATION) BY THE AVAILABLE AMOUNT OF CHARGED tRNA MOLECULES – THE MODEL

The proposed model is mainly based on 3 prerequisites.

(i) Plastid protein synthesis depends on the amount of aminoacyl-tRNAs which are formed by aminoacylation of plastid tRNAs by nuclear encoded aminoacyl-tRNA synthetases.

(ii) The competitive use of glutamyl-$tRNA^{Glu}_{GAA}$ in protein and chlorophyll synthesis limits the supply of this particular aminoacyl-tRNA in early phases of chloroplast differentiation. Neither $tRNA^{Glu}_{GAA}$ nor glutamyl-tRNA synthetase appears immediately upon illumination; thus, glutamyl-$tRNA^{Glu}_{GAA}$ is not available during the early stage of chloroplast development.

(iii) The differential effect of limiting amounts of glutamyl-$tRNA^{Glu}_{GAA}$ on translation of plastid messages depends on the frequencies of glutamate codons in the transcripts.

3.1. *Dependence of plastid protein synthesis on nuclear-encoded aminoacyl-tRNA synthetases*

Regulation of protein synthesis can result from varying amounts of each constituent participating in the whole process [71–73]. Aminoacyl-tRNAs are formed by acylation of plastid tRNAs with the cognate amino acids by means of nuclear-coded aminoacyl-tRNA synthetases [19,74]. The light-induced de novo synthesis of enzymes [29–32] takes place on cytoplasmic ribosomes [30,33,34]. It is preceded by a transient rise of the corresponding in vitro translatable mRNAs [12]. After synthesis the precursor polypeptides are very probably transported posttranslationally into chloroplasts as concluded from in vitro translocation and processing of one particular *Euglena* chloroplast aminoacyl-tRNA synthetase, i.e. leucyl-tRNA synthetase [27]. Dark-grown, chemoorganotrophic cells illuminated for 12 h in the presence of carbon dioxide contain approximately 70% of the enzyme activity finally accumulated in photoautotrophic cells [12]. At this time chlorophyll synthesis starts to rise [75]. The amount of certain thylakoid membrane proteins increases linearly [21,42], while the accumulation of several stroma proteins (e.g. large subunits of RuBPCase [76,77]) lags behind.

There is only one exceptional aminoacyl-tRNA, namely glutamyl-tRNA$^{Glu}_{GAA}$, which is used not only for protein synthesis but also for 5-aminolevulinic acid formation in tetrapyrrole pigment biosynthesis [15,24]. The limited amount of glutamyl-tRNA$^{Glu}_{GAA}$ in the first 10–12 h of chloroplast development, which results from the limiting amounts of both the tRNA$^{Glu}_{GAA}$ [31] and glutamyl-tRNA synthetase [12,31] could explain the differential rates of synthesis of proteins if polysome-bound messages contain different frequencies of glutamate codons.

Table I

Frequency of GAA- and GAG-glutamate codons in *Euglena* plastid protein genes

Gene	Percent glutamate codons			Ref.
	GAA	GAG	Total	
psaA	1.7	0.5	2.2	46
psaB	2.0	0.8	2.8	47
psbA	5.5	0.6	4.1	41
psbB	3.3	1.0	4.3	80
psbC[a]	1.8	0.0	1.8	44
psbE	4.8	0.0	4.8	47
psbF	0.0	0.0	0.0	47
atpH	5.1	0.0	5.1	43
tufA	6.6	0.7	7.3	52
rbcL	5.7	1.1	6.8	53,54
rps 3	1.8	0.5	2.3	50
rps 7	6.4	1.3	7.7	48
rps 12	2.4	0.0	3.1	48
rpl 2	1.1	0.0	1.1	50
rpl 19	3.1	0.0	3.1	50
rpl 20	1.6	0.0	1.6	49
rpl 22	2.6	0.0	2.6	50
rpl 23	2.0	1.0	3.0	50
rpoC[b]	–	–	5.7	51

[a] Only part of the gene structure is known

[b] Since only part of the derived amino acid and not gene sequence has been published the total percentage of glutamate codons is indicated

3.2. *Sequence analysis of known* Euglena *plastid protein genes*

Table I summarizes the glutamate codon usage in sequenced *Euglena* protein genes coded for by plastid DNA. Two features are remarkable: (i) the GAA-codon is much more frequently found than the GAG-codon in all selected genes; and (ii) the genes differ with respect to the glutamate codon frequency.

Three groups of genes referred to as low, intermediate and high frequency can be discerned. All known genes for ribosomal proteins except rps 7 and all known psa genes belong to the low frequency group (1.1–3.1% glutamate codons). The genes for tufA, rbcL, rps7 and probably rpoC (only part of the coding sequence is known in the latter case) contain approximately 3 times more of these codons (high frequency, 6.8–7.3%). An additional accumulation of the glutamate codons in direct repeats of 2 or 3 codons (rbcL [54]; psbA [41]) is furthermore observed only in these genes. The protein genes psbE [47] and atpH [43] contain an intermediate percentage of glutamate codons (4.1% and 5.1%, respectively).

3.3. *Translational regulation of plastid protein synthesis at the step of elongation by limiting amounts of glutamyl-tRNA$^{Glu}_{GAA}$*

Assuming that equal proportions of psaA, rbcL or psbC transcripts are bound to polysomes (light-activated polysome formation, a term taken from Heizmann et al. [62] to describe the assembly of mRNAs with preexisting ribosomes), the rate of their translation should depend on the frequency of glutamate codons if the amount of glutamyl-tRNA$^{Glu}_{GAA}$ is limiting. Translation of mRNAs with a low number of glutamate codons should be less affected by the limited supply of glutamyl-tRNA$^{Glu}_{GAA}$ than elongation of transcripts with a high frequency of glutamate codons.

The rate of translation of the psaA or psbC transcript then would be higher than those of the rbcL or tufA mRNAs. In this way accumulation of ribulose-1,5-bisphosphate carboxylase and elongation factor Tu would follow synthesis of membrane proteins required for binding of chlorophyll whose synthesis starts after a 10-h lag-period. Consequently, establishment of photosystem reaction centres and the proton translocating ATPase (one subunit is the atpH gene product) required for electron transport and thus energy conversion would precede synthesis of stroma proteins involved in carbon fixation and metabolism in the first hours of chloroplast development. Indeed, this

predicted temporal pattern of appearance of polypeptides has been demonstrated experimentally ([21,42,63]; cf. Fig. 1). In spite of concomitant polysomal association of psbA, rbcL, psbB and psbC transcripts [21,26,63] synthesis of plastid polypeptides starts with formation of thylakoid proteins required for chlorophyll binding and is followed by accumulation of stroma proteins, which are involved in carbon dioxide fixation.

In the later phases of chloroplast development (after 48 h of light exposure), plastid polypeptides of the gene expression apparatus like elongation factor Tu or β-subunit of the soluble RNA-polymerase are formed. During this stage the amount of glutamyl-$tRNA^{Glu}_{GAA}$ probably is no longer limiting for translational elongation, since the amount of light-induced plastid tRNAs as well as nuclear-encoded aminoacyl-tRNA synthetases has been increased several-fold. Assembly of ribosomal proteins into ribosomes, which depends on the proper balance of ribosomal tRNAs and proteins, contributes to the light-induced plastid polysome formation (this phenomenon was first described for cytoplasmic polysomes in *Euglena* [62]). In contrast to light-activated polysome formation, this process is characterized by the association of polysomes from newly formed transcripts and ribosomes.

The proposed mechanism of translational regulation at the step of elongation by limitation of glutamyl-$tRNA^{Glu}_{GAA}$ becomes still more complicated if one takes into account that one intermediate in chlorophyll synthesis, namely protochlorophyllide, is the prosthetic group of the putative blue-red light plastid photoreceptor in *Euglena* [78,79]. It is thought to control plastid gene expression [3]. Regeneration of the depleted photoreceptor after transformation of protein-bound protochlorophyllide into chlorophyllide [14] could only be achieved after the capacity for chlorophyll biosynthesis [15,24] has been established inside chloroplasts.

The proposed model of translationally controlled gene expression in plastids of *Euglena* might at least partially explain the observed fine tuning in temporal and spatial organisation of the developing plastid. Though it is difficult to investigate the whole model experimentally, the effect of limiting amounts of certain aminoacyl-tRNAs on translation of in vitro-transcribed plastid genes could be studied directly in a tRNA-depleted in vitro translation system [79].

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