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Expression of the Chloroplast Genome: Modern Concepts and Experimental Approaches

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Abstract—A unique feature of plants is the presence of two extra-nuclear genomes of chloroplasts and mitochondria. The chloroplast (cp) genome is relatively small and contains only 100–120 genes, which encode less than 5% of all proteins required for plastid to function. Expression of the cpDNA retains certain prokaryotic features, such as gene cotranscription within the operon, bacteria-like RNA polymerases and promoters, and 70S ribosomes. However, eukaryotic features also appear in this process, such as the uncoupling of transcription and translation, the involvement of phage-type RNA polymerases, RNA editing, and splicing of the primary transcripts. The interaction between the nucleus (nuclear genome) and cytoplasm (plastid and mitochondrial genomes) during plant development is necessary for proper development and adaptation to the environment. The aim of this review is to disclose the peculiarities of plastid genome expression. The way how the genetic information in chloroplasts is used (transcription, editing, splicing, polyadenylation, and translation) is consequently described. Furthermore, the importance of all expression machinery components in plant life is discussed. Modern approaches for RNA pool studies are described, and the critical points of the nuclear-cytoplasmic interactions in the chloroplast function are revealed. Information about the most important factors of nuclear-cytoplasmic signaling in higher plants (sigma factors and PPR proteins encoded by the nucleus) are reviewed. Thus, the multilevelness and viability of regulating the plastid genome expression in plant cells and the interdependence of the processes in different compartments is proved. A summary of the latest studies of the expression of plastid genome using genetic chips (microarrays and macroarrays) is described. The original results are presented.

Keywords: chloroplast, plastids, expression, transcription, RNA polymerases, editing, splicing, translation, microarray, macroarray

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The presence of plastids in a cell is one of the major unique properties of plants. In addition to performing photosynthetic functions, plastids are involved in a number of other vital cellular processes vie the synthesis of starch, fatty acids, amino acids, and pigments (Wicke et al., 2011). A plant's chloroplast genome consists of a double-stranded DNA that average in size from 130 to180 bp and vary in copy number from 8 and 1000 copies per plastid, with up to 50 plastids per cell. In barley, the chloroplast genome constitutes 136462 bp; in wheat, 134545 bp. Currently, GenBank (http://www.ncbi.nlm.nih.gov/genomes/GenomesGroup.cgi?taxid=2759&opt=plastid) contains more than 900 primary nucleotide sequences for plastomes in eukaryotes, of which about 700 belong to the Viridiplantae group, which includes higher terrestrial plants. Most plastomes were sequenced after 2006, when wide scale sequencing methods were developed and the cost of analysis (sequencing) decreased dramatically. Plastomes of photosynthetic plants contain from 70 (angiosperms) to 88 (mosses) protein coding genes: 33 (most dicots), 34 (monocots), and 35 (mosses) structural RNA genes and thus, overall, 100–120 genes (Wakasugi et al., 1994; Ohyama, 1996; Bock, 2007). Table 1 shows a typical set of genes of the chloroplast DNA of higher plants on the example of wheat (Ogihara et al., 2000).

It is assumed that the functioning of plastids in higher plants requires more than 2100 proteins (Leis-

Abbreviations: cpDNA—chloroplast DNA; PEP—plastid—encoded plastid RNA polymerase; NEP—nuclear-encoded plastid RNA polymerase; PSI—photosystem I; PSII—photosystem II; dRNA-seq—differential RNA sequencing; σ-factor—sigma factor; SIG1-SIG6—sigma factors of arabidopsis; cpCK2—chloroplast casein kinase 2; UTR—untranslated region of the transcript; ncRNAs—non-coding RNA; PNPase—polynucleotide phosphorylase; RNase—ribonuclease; IR—inverted repeat; PPR proteins—proteins with pentatricopeptide repeats; TPR proteins—proteins with tetratrico peptide repeat; MORF—multiple sites organellar RNA editing factors; CRM protein—Chloroplast RNA splicing and ribosome maturation protein; SD—Shine-Dalgarno sequence; qRT-PCR—PCR in real time; RT-PCR—polymerase chain reaction after reverse transcription.

ter, 2003), and only less than 5% of these are encoded by their own genome (Shiina et al., 2005). Biogenesis and differentiation of plastids depends on the coordinated expression of the nuclear and plastid genes (Gray et al., 2003). Regulation of plastid genome expression may be carried out on the DNA level based on changes in the copy number of plastome per organelle. However, mostly, the expression of plastid genome is modulated by different processes that occur during and after transcription, during translation and post-translationally (Zhelyazkova, 2012).

Chloroplasts appeared in plant cell as a result of the endosymbiosis of primitive single cell eukaryotic organisms with photosynthetic prokaryotes (Danilenko and Davydenko, 2003). Thus, it is not surprising that the expression of the plastid genome retains features of prokaryotes: operon organization (cotranscription of genes), RNA polymerases and promoters similar to bacteria, the mRNA structure, the presence of 70S ribosomes, and others. However, plastid genomes have also acquired novel properties, such as uncoupled transcription and translation, and the modification of primary transcripts as a result of editing and splicing (Barkan, 2011; Cardi et al., 2012).

Transcription of the plastid genome is a complex process that is important for the development and adaptive regulation of its functions. A number of molecules are involved in the transcriptional regulation of plastids: RNA polymerases, sigma-factors, transcription factors, plastid nucleoid proteins, and various signaling molecules (Shiina et al., 2005). Transcription of plastid genome is also largely significantly on the expression of nuclear genome.

Transcription of plastid genes in higher plants is performed by two different types of polymerases: bacterial type RNA polymerase encoded by plastids (PEP) and a phage-like nuclear-encoded RNA polymerase (NEP), which recognize different types of promoters and differ in transcriptional activity in different types of plastids (Börner et al., 2015). More than 60% of plastid genes are read as sufficiently stable multicistronic (polycistronic) complexes. Plastid operons are conserved across different plant species (Kapoor and Sugira, 1998), and are present as mono-, di- and polycistronic complexes.

Thus, of the 113 genes of the chloroplast genome of barley, 86 are part of 20 operons (see Table 2) and 27 genes are transcribed as monocistronic (Zhelyazkova et al., 2012).

Genes encoding subunits of the same complex, or proteins with common functions, in some cases are read as part of a single operon, which determines their coordinated function and stoichiometric accumulation. This feature promotes a differential expression of the genes of the transcriptional/translational machinery in comparison to genes encoding photosynthetic proteins (Baumgartner et al., 1993).

Most genes of chloroplast DNA (cpDNA) can be transcribed by both types of polymerases, NEP and PEP, but from different promoters (Hajdukiewicz et al., 1997; Liere and Börner, 2007; Barkan, 2011). The macroarray analysis of tobacco genome revealed that in mutant plants defective for plastid polymerase (PEP), nuclear RNA polymerase (NEP) can transcribe the entire plastid genome, though into polymerase-specific profiles. This study revealed not just quantitative but also qualitative differences between transcripts in normal and PEP-defective plants (Legen et al., 2002). Apparently, the type of polymerase that synthesizes the transcript, in many cases determines its fate: will it be read as a normal protein? The presence of any one type of polymerase, NEP or PEP, is not sufficient for the biogenesis of photosynthetically competent chloroplasts, especially, as some chloroplast genes require transcription by a specific polymerase to achieve the appropriate level of expression. However, the loss of PEP activity is less traumatic for a plant (Allison et al., 1996; Hess and Börner, 1999; Swiatecka-Hagenbruch et al., 2008).

NEP can be represented by two types of RNA polymerases: RpoTp (functioning in plastids) and RpoTmp (operates in the mitochondria and in plastids in dicots). Functional significance of RpoTp has been shown both at the early and late stages of vegetative plant development (in arabidopsis). RpoTmp is especially important during early stages in arabidopsis, when it performs the transcription of the rrn operon (Courtois et al., 2007).

Recently developed molecular biological methodologies permit the simultaneous analysis of the transcripts accumulation for a large number of genes in various samples using micro and macro arrays. A number of published reports present genomic studies of organelles by microarray and macroarray approaches that allow deep investigations of the expression apparatus in plant cells.

A comprehensive study of plastid transcriptome during the development and ripening of a tomato, accompanied by chloroplast–chromoplast convertion, uncovered that most plastid genes are inhibited to a greater extent in fruits than in leaves. Differentiation from chloroplast to chromoplast (in tomato fruits) does not introduce significant changes in the level of accumulation of plastid transcripts. Transcriptional and translational inhibitions (negative regulation) were more pronounced for genes associated with photosynthesis compared to the genes involved in the transcription. *accD* is the only plastid gene (part of the cycle of biosynthesis of fatty acids), which was actively expressed. Apparently, for its functioning expression activity in chromoplasts was maintained (Kahlau and Bock, 2008).

Similar results were obtained when comparing the levels of transcript accumulation in potato leaves and tubers: most genes were inhibited in amyloplasts of

Table 1. Composition of wheat chloroplast genome (from Ogihara et al., 2000; 2002)

Final product	Gene designations	Gene product information
RNA	*23S rDNA, 16S rDNA, 5S rDNA, 4.5S rDNA*	Ribosomal genes
	trn A, trnC, trnD, trnE, trnF, trnG, trnH, trnI, trnK, trnL, trnM (trnfM), trnN, trnP, trnQ, trnR, trnS, trnT, trV, trW, trnY	tRNA genes (30 types, corresponding to 20 aminoacids)
Proteins of photosynthetic system	*PsaA, -B, -C, -I, -J*	Photosystem I
	PsbA, -B, -C, -D, -E, -F, -H, -I, -J,-K, -L,-M, -N, -T	Photosystem II
	PetA, -B, -D, -G	Cytochromes
	AtpA, -B, -E, -F, -H, -I	ATP synthase
	rbcL	Large subunit of ribuloso-biphosphate-carboxylase
Ribosomal proteins	*rpl 2, rpl14, rpl16, rpl20, rpl22, rpl23, rpl32, rpl33, rpl36*	Large ribosome subunit
	rps 2, rps3, rps4, rps7, rps8, rps11, rps12, rps14, rps15, rps16, rps18, rps19	Small ribosome subunit
Proteins of the transcription/translation apparatus	*rpoA, rpoB, rpoC1, rpoC2*	Subunits of RNA polimerase
	infA	Translation factor
Other proteins	*ndhA, ndhB, ndhC, ndhD, ndhE, ndhF, ndhG, ndhH, ndhI, ndhJ, ndhK*	Subunits of NADH dehydrogenase
	clpP	Proteinase
	cemA	Chloroplast membrane proteins
	matK	Maturase
	ycf3, ycf4, ycf5, ycf6, ycf9	Open reading frames, conserved between cereals' plastomes

tubers compared to leaves. Common (identical) transcription initiation sites were identified for the genes transcribed in the chloroplast and amyloplasts. The emergence of new sites unique to the leaves or tubers was also noted. In addition, differences were observed between the use of promoters in the two types of organelles. In general, the association of transcripts with ribosomes was lower in amyloplasts. However, a fairly high ribosome association was observed for the *accD* transcript. The results of the two studies described above indicate the existence of common organelle expression regulation mechanisms for tuber amyloplasts and chromoplasts in the fruit (Valkov et al., 2009).

Studies in *Nicotiana tabacum* plants showed that the levels of gene transcripts encoding for subunits of the photosynthetic proteins growing in light conditions are significantly higher than in the dark. About 60% of the probes to photosynthetically significant genes at least doubled in the quantity of transcripts in tissues growing in the light (Nakamura et al., 2003a).

Studies of the steady-state transcript levels in wheat uncovered that at the initial stages of development (imbibition/germination), the level of gene transcripts of the photosystem I (PSI) is significantly lower than that of photosystem II (PSII) (Siniauskaya et al., 2008). This makes good biological sense since PSII develops and begins to operate earlier than PSI.

Comparison of plastid transcriptomes in leaves and female flowers in a cucumber plant revealed a significant increase in the number of transcripts in flowers: in particular, for 13 ribosomal protein genes, *rpoA*, *clpP*, *ycf1*, *ycf2*, and *ycf15*. At the same time, strong repression of photosynthetic genes was detected. The most striking example was finding that transcript levels for 8 *psb* (PSII) genes were significantly reduced . The only *ndh* gene with increased expression level was *ndhH* (Zmienko et al., 2011).

Analysis of the transcript pools at the apical tip and basal part of the leaf in the corn showed that the RNA of photosynthetically important genes present major part at the tip of the leaf, while in the basal transcripts of energy exchange genes predominate (Cahoon et al., 2008).

Table 2. Potential mono- or polycistronic transcription complexes (operons) of plastid genes on the example of barley (from Zhelyazkova et al., 2012)

Transcription complexes	
Characteristic	Composition
Monocistronic	*ndhF*, *psbA*, *psbM*, *rbcL*, *rpl23*, *rps16*, *psaI*, *psbN*, *petN*, *trnG-GGC*, *trnT-GGU*, *trnD-GUC*, *trnS-GGA*, *trnL-UAA*, *trnF-GAA*, *trnM-CAU*, *trnH-GUG*, *trnV-GAC*, *ccsA*, *trnN-GUU*, *trnL-CAA*, *trnP-UGG*, *trnW-CCA*, *trnC-GCA*, *trnS-UGA*, *trnS-GCU*, *trnQ-UGG*
Dicistronic and polycistronic	Consists of genes with similar or related functions
	psbE-psbF—psbL-psbJ
	psbK-psbI-psbD—psbC-psbZ
	trnG-UCC-trnfM-CAU
	rpoB-rpoC1-rpoC2
	trnE-UUC-trnY-GUA
	Consists of genes with geterologic functions
	clpP-rps12 5'-rpl20
	petL-petG-psaJ-rpl33-rps18
	psaA-psaB-rps14-trnfM-CAU-trnR-UCU
	psbB-psbT-psbH-petB—petD
	atpB-atpE-trnV-UAC—ndhC-ndhK-ndhJ
	rpl32-trnL-UAG
	trnT-UGU-rps4-ycf3
	ndhH-ndhA—ndhI-ndhG-ndhE-psaC-ndhD
	rps2-atpI-atpH-atpF-atpA
	ycf4-cemA—petA
	trnK-UUU-matK
	rps12 3'-rps7-ndhB
	trnI-CAU-rpl23-rpl2-rps19-rpl22-rps3-rpl16- rpl14-rps8-infA-rpl36-rps11-rpoA
	rrn16-trnI-GAU-trnA-UGC-rrn23-rrn4.5-rrn5- trnR-ACG-rps15—ndhH

Genes within an operon are underlined (e.g. *psbK*), from which transcription can be initiated.

Further progress in the study of the transcriptomes of higher plants (barley) was achieved through the study of Zhelyazkova and colleagues (2012). The primary plastid transcripts were analyzed with the application of the method of differential RNA sequencing (dRNA-seq) to compare two cDNA libraries obtained from normal green barley plastids and white plastids of the mutant *albostrians* barley. This experiment specifically included plastome RNA from the leaves of the white barley mutant (albostrians) in order to identify features distinct between NEP and PEP in plastids. It turned out that only 11 genes of barley plastids, *trnL-UAA*, *trnM-CAU*, *trnN-GUU*, *trnT*, *trnS-UGA*, *trnQ-UGG*, *psbE-F-L-J*, and *petN*, are transcribed exclusively by PEP. It was shown that PEP is the dominant plastid polymerase in mature barley leaves and 88% TSS (Transcription Start Site) in green barley leaves are associated with PEP. The results of dRNA-seq showed that cpDNA contains considerably higher number of promoters than genes. Therefore, the presence of promoters to both polymerases is characteristic for plastid genes. Perhaps, this has an adaptive function. Thus, in plant plastids, multiple promoters trigger the transcription of individual genes and operons. As a result, different transcripts of the same gene are generated, which is required for proper gene functioning, allowing plants to adapt quickly to changes in the external and internal conditions. Moreover, the identification of multiple transcription initiation sites inside the operons (see Table 2) points to the potential for the transcriptional separation of genes within a polycistronic cluster (Zhelyazkova et al., 2012). This is the path for obtaining less complex transcripts and for increasing the number of individual mRNAs tran-

scribed from the same operon. Both processes can contribute to the differential expression of genes within the same operon.

The intensity of the transcription of individual genes in the context of the same operon is highly conserved, although particular sites of the same operon may be transcribed differently (Aleinikova et al., 2011). As it was shown on barley, genes within operons *rrn16*, *rps2*, *psaA*, and *atpB*, which include functionally unrelated binding proteins and RNA, are transcribed differently (Aleinikova, 2012). Operon *atpB-atpE-trnV-ndhC-ndhK-ndhJ* is characterized by a much greater intensity of transcription (by a factor of at least three) for genes *atpB* and *trnV* compared to other genes. In the *psaA* operon, the first two genes are transcribed uniformly, while the *rps14* gene, associated functionally with another group, is transcribed at a significantly higher intensity. These studies confirm the differential transcriptional regulation of individual genes within the operons (Aleinikova, 2012).

The initiation of transcription is a crucial stage in genome expression in many organisms. It was believed previously that transcription does not play a significant role in the regulation of gene expression in plastids and posttranscriptional processes are more important. These representations were revised after the discovery and studies of σ-factors (sigma-factors). σ-factors are nuclear encoded proteins that confer promoter specificity to the PEP complex. In the PEP enzymatic complex (of the prokaryotic type), σ-factor functions as a subunit that recognizes the promoter regions of the target genes (Toyoshima et al., 2005). σ-factors interact with RNA polymerases in two processes that determine the success and effectiveness of transcription: in promoter recognition and DNA melting (Lerbs-Mache, 2011).

Different σ-factors have specific functions in the regulation of plastid genome expression and are responsible for the transcription of a particular set of genes (Yagi and Shiina, 2014). The variety of σ-factors and their differential use by plants depending on environmental signals, stages of organismal development, and the type of plastid provide the appropriate type of regulation of gene transcription (Allison, 2000; Toyoshima et al., 2005; Liere and Börner, 2007; Lerbs-Mache, 2011).

It has been proposed that the presence of multiple promoters and σ-factors in chloroplasts may be necessary to maintain the functional state of the chloroplast genetic system while the mutations arise (Maier et al., 2008) or, more likely, to ensure the coordinated work of the whole transcriptional apparatus in variable conditions (Lerbs-Mache, 2011). It is possible that both assumptions with respect to the functional significance of the multiplicity of promoters and the σ-factor in chloroplasts reflect different sides of the transcription process, whose features are not totally understood.

All known plant σ-factors belong to the σ_{70} group (primary sigma factors). Most genomes of higher plants encode six σ-factors (Lyska et al., 2013). In *Arabidopsis thaliana* (*A. thaliana*), of the six σσ-factors SIG1–SIG6, two (SIG2 and SIG6) are vitally important for the appropriate functioning of its plastids (photoautotrophic growth). Presumably, the SIG1 function contributes to the fast adaptation of PSI activity to the daily changes in the intensity of illumination and may also play a role in the host-pathogen response (Lerbs-Mache, 2011). SIG2 is involved in promoter recognition and specific transcription of certain tRNA genes, and *psaJ*, *psbD*, *psbA*, and *rbcL* (based on the analysis of arabidopsis cDNA microchips). SIG3 provides for the specific initiation of the transcription from the promoter of the *psbN* gene and can also influence the expression of the *psbB* operon through the regulation of the *psbT* transcript (an antisense transcript generated from a different DNA strand in the opposite direction) (Zghidi et al., 2007). SIG4 is especially significant for the transcription of the *ndhF* gene. SIG5 is required for the recognition of a blue light-dependnt promoter of the *psbD* gene and is also important for the circadian regulation of the transcription of individual chloroplast genes (Noordally et al., 2013). SIG6 plays a global role during the early stages of plastid differentiation and plant development (Lerbs-Mache, 2011). Summary information on the σ-factors and their functions in plants is provided in Table 3.

The expression of the plastid genome is affected by modifications of the σ-factors through phosphorylation. The most important regulator of σ-factor activity and, consequently, transcription, is the nuclear encoded chloroplast casein kinase 2 (cpCK2) (Schweer et al., 2010).

A recent study reported a detailed investigation of gene interactions between the ATP synthase complex (important for photosynthetic processes and respiration) and σ-factors (Ghulam et al., 2012). In higher plants, the genes of ATP synthase complex are separated and organized in two operons: the large (*atpI/H/A*), and small (*atpB/E*) operon. Studies in arabidopsis revealed how the physical isolation of the genes of the ATP synthase complex (atp) is overcome in the chloroplast cluster and how their transcription is coordinated. Both promoters for atp operons are PEP-dependent and require σ-factors for specific promoter recognition. The transcription of these operons is initiated by the same σ-factor, SIG2. SIG2 provides for the base level of the mRNA synthesis of the *atp* genes, which encode for different subunits of ATP synthase. Further, transcriptional initiation of the large and small *atp* operons is executed by the σ-factors SIG3 and SIG6, respectively, which modulate the expression of the *atp* gene, depending on the physiological and environmental conditions. The combination of the transcriptional regulation of the *atpH* mRNA by SIG3 factor and the specific stabilization of these transcripts through interaction with the PPR10 protein probably represent the mechanisms by which

Table 3. Plant sigma-factors and their functional role in plastids (Ex: arabidopsis) (from Lerbs-Mache, 2011, with additions)

Arabidopsis gene encoding for σ-factor	σ-factor	Biochemical process	Biological function in plastids
At1g64860	SIG1	Phosphorylation Interaction with SIB1*	Fast adaptation of PS1 activity to the changes in light intensity Transcription of *psaA*, *psbB*, *psbE* (Tozawa et al., 2007)
At1g08540	SIG2		Regulation of transcription and biosynthesis of chlorophyll through transcription of tRNA
			Stabilization of PS1 through transcription of *psaJ*
			Overcoming physical separation in the cpDNA *atp* cluster, and its transcription (Ghulam et al., 2012)
			Switching of RNA polymerases from NEP to PEP through interaction with RPOTp
At3g53920	SIG3	Proteolytic cleavage	Specific transcription of *psbN*—regulation of expression of *psbT* through production of antisense RNA
			Participation in transcriptional initiation of the large *atp* cluster *atpI/H/F/A* (Ghulam et al., 2012)
At5g13730	SIG4		Specific transcription of *ndnF*
At5g24120	SIG5		Specific transcription of *psbD* gene from promoter sensitive to blue light. Circadian regulation of transcription of individual chloroplasts genes
At2g36990	SIG6	Phosphorylation, interaction with DG1**	Phosphorylation, interaction with DG1** Participation in transcriptional initiation of the small *atp* cluster *atpB/atpE* at the late stages of plant development (Ghulam et al., 2012)

* SIB1—SIG1 interacting protein, plays a protective role in plants' response.
** DG1—PPR-interacting protein SIG6, performs a regulatory function.

chloroplasts control the expression of the *atpH* gene encoding for the C subunit and the size of the C ring in the ATP-synthase.

It is known that depending on the species, the number of C subunits in the ATP-synthase ring can vary from 10 to 15 (Stock et al., 1999; Pogoryelov et al., 2005, 2007, Ghulam et al., 2012).

The number of C subunits is a very important parameter for the ATP-synthase complex, as it defines the number of H+ (protons) that are translocated through the membrane to support ATP synthesis. A very interesting hypothesis is that an increased size of the C ring may be the price that the plants pay for the synthesis of ATP in adverse conditions. It is possible that chloroplasts possess a regulatory mechanism to increase the efficiency of the ATP-synthase by changing the number of C subunits under the impact of various stress factors (Ghulam et al., 2012).

Expression of Plastid Genome During Ontogenesis

The cascade activation model of the plasmon through NEP was originially proposed (Liere and Maliga, 2001). It was considered that NEP activity is required for the initiation of PEP at the early stages of chloroplast development by the transcription of the operon containing the *rpoA* and *rpoB* genes, which encode subunits of PEP. Then, NEP is increasingly replaced by PEP and the latter selectively transcribes the genes of the photosynthetic complexes. As mature photosynthetic chloroplasts appear, PEP activity is reduced to the steady-state level. This hypothesis explains gene regulation in plastid ontogenesis reasonably well. However, the results of many subsequent transcription studies testified otherwise.

The experiments on maize by Cahoon and colleagues (2004) uncovered that as chloroplasts develop, the activities of both types of polymerases increase; however, there is a difference in the stability of their transcripts. The levels of the NEP enzyme are reduced as plants grow older and the increased destabilization of the NEP transcripts is observed. However, due to the increased activity of this polymerase in mature chloroplasts, the levels of NEP produced mRNA in the cell remain approximately the same (Cahoon et al., 2004). The transcriptional activity of PEP increases in

the course of chloroplast development concomitant with the constant or even increased stability of its transcripts. Thus, Cahoon and colleagues (2004) pointed a characteristic feature of plastid genome expression during ontogenesis: the difference in the accumulation of gene transcripts produced by the two polymerases, NEP and PEP. During plastid development, the levels of NEP transcripts remain practically unchanged, while the levels of PEP transcripts increase.

Next, studies in arabidopsis and spinach revealed that NEP and PEP are already present in the seeds. Treatment with a specific inhibitor of PEP activity, Tagetin, confirmed that PEP is required for effective seed germination, as it provides the transcription of ribosomal RNA (Demarsy et al., 2006). Same investigators reported that during arabidopsis seed germination, all three polymerases, NEP (RpoTp, RpoTmp, and PEP), actively synthesize the new plastid mRNA already at the stage of imbibition/seed stratification (stage 0+). RpoTp transcribes the genes of ribosomal proteins and PEP subunits, while RpoTmp and PEP transcribe the rRNA operon. Moving to light (at the germination stages after 0+) initiates the PEP-mediated transcription of photosynthetically significant genes (*rbcL* is transcribed first). During further seedling development (stages 1–2), PEP continues the active transcription of the genes of PSI, PSII, and the electron transport chain (Demarsy et al., 2012).

The number of NEP-synthesized transcripts for genes of PEP subunits and ribosome proteins abruptly stops growing and starts declining from stage 0+, and at stage 1 (the appearance of roots), is maintained at a certain stable level or decreases. The phase of the highest NEP activity, which falls at the early stages of seed germination (shown in arabidopsis), is characterized by a high level of transcription for the whole plastid genome resulting in the output (read out) of antisense RNA from genes localized on the opposite DNA strand. Notably, the quantitative ratio of sense and antisense RNA for the overwhelming majority of plastid mRNAs changed depending on the stage of plant development and plastid differentiation. The stratification stage and appearance of the root (0–1) were characterized by high levels of antisense RNA and small value of the ratio of sense to antisense RNA (sense/antisense). In green tissues (stages 2–4: root growth, the greening of seedlings, and the opening of cotyledons) for most plastid mRNAs, the levels of sense transcripts are significantly greater than antisense; thus, the sense/antisense RNA ratio is increased (Demarsy et al., 2012). The functional significance of antisense RNA transcription is not clear. It may have a regulatory function for the switching of polymerase from NEP to PEP or it may be a side effect of this process.

A characteristic feature of gene expression in chloroplasts of terrestrial plants is the complexity of the RNA molecule population (pool) that are produced during the transcription of most genes (Barkan, 2011). The pool of plastid RNA contains primary and processed (mature) transcripts. The diversity of the transcripts in chloroplasts is generated during the initiation of transcription not from a single but from different promoters for the same genes, often followed by RNA processing at a plurality of different sites. An example that demonstrates the possibility of accumulating different transcripts for a single gene cluster is the *psbB* operon (Barkan, 1988; Westhoff and Hermann, 1988). A single probe to this coding region allows us to identify at least 15 types of transcripts (Stern et al., 2010).

The processes that occur subsequent to RNA transcription, RNA stabilization and degradation of transcripts, are even more significant in the regulation of the plastid genome expression (and, thus, the plastid function) than transcription per se (Del Campo, 2009).

RNA Processing

The primary transcripts of chloroplast genes are read as polycistronic molecules, which are cut into individual transcripts and, then, their 5'- and 3'-ends are subjected to modifications (maturation). A 5'-UTR (5' untranslated regions) and a 3'-UTR sequences prevent the rapid degradation of the primary transcripts, ensuring their stability (Del Campo, 2009). They are necessary for the posttranslational regulation of gene expression (Stern et al., 2010; Zhelyzkova et al., 2012).

The unprocessed (primary) 5'-ends of chloroplast transcripts carry 5'-di- or triphosphates. The processed chloroplast transcripts have monophosphorylated 5'-ends (Zhelyzkova et al., 2012). These are formed by two possible mechanisms during mRNA maturation: a 5'-3' exonucleolytic pathway or site-specific cleavage by endoribonucleases (Stern et al., 2010).

It is believed that the major mechanism for the maturation of the 5'-ends is the endonucleolytic pathway. However, evidence has also been presented in favor of another assumption. These mechanisms may involve RNase J or, less likely, RNase E. RNase J is the main ribonuclease responsible for the maturation of the 5'-end portions of chloroplast transcripts on which RNA-binding proteins (pentatricopeptide repeat (PPR) proteins encoded in the nucleus) function as barriers for its activity (Luro et al., 2013). Thus, the degree of 5'-processing of the transcript is determined by PPR-proteins and by the secondary structure of the RNA molecule itself (Stern et al., 2010).

The transcriptional termination in chloroplasts is ineffective. Thus, most 3'-ends of mature plastid mRNA are formed by processing the primary transcript. Processing the 3'-terminal regions involves exso- and endonucleases, and RNA-binding proteins. Two plant chloroplast exsoribonucleases, PNPase and

RNR1 (RNase R), are well studied. The 3'-ends are formed mainly thanks to the 3'-5' exoribonuclease activity of the polynucleotide phosphorylase (PNPase). This enzyme is sensitive to the presence of secondary RNA structures and terminal IR (inverted repeats). Thus, it is inhibited at the 3' stem-loop structures (Yehudai-Resheff et al., 2001, Lyska et al., 2013). The significance of this enzyme can be seen by the fact that maturation of the 3'-ends of the *rbcL* and *psbA* mRNA is incomplete in plants that lack PNPase (Walter et al., 2002).

Some chloroplast mRNA do not form 3' stem-loop structures. These mRNA are prime candidates for stabilization using small noncoding RNAs (ncRNAs). They are found in large quantities in chloroplasts of different plants (Hotto et al., 2011; Zhelyzkova et al., 2012). In plastids, ncRNAs are synthesized both from intergenic regions and in the form of antisense transcripts (for approximately 35% of all genes in green plastids). According to Hotto and colleagues (2011), arabidopsis contains at least 39 chloroplast ncRNA complementary to the 3'-ends of the sense chloroplast mRNA. In bacteria, ncRNA binding to mRNA 3'-ends stabilizes these mRNA by blocking the function of 3'-5'-exoribonucleaze (Opdyke et al., 2004). It is possible that a similar process occurs in chloroplasts. The simplest example of RNA stabilization by ncRNA is the antisense RNA of the *psbT* gene, whose arising stabilizes the sense *psbT* transcript through the formation of a double-stranded RNA/RNA hybrid. This promotes the inhibition of the *psbT* mRNA translation and protection from nucleolytic degradation under conditions of oxidative stress (Zghidi-Abouzid et al., 2011).

It is assumed that each small RNA corresponds to a site of PPR-protein binding (as a "footprint" of the PPR-protein). One of the well documented functions of these proteins is to protect the adjacent RNA from degradation by exonucleases (Loiselay et al., 2008; Zhelyazkova et al., 2012). Thus, the transcript is stabilized by binding with the PPR proteins. This mechanism has been described for PPR10, CRP1, and HCF152 proteins (Barkan et al., 1994; Meierhoff et al., 2003; Nakamura et al., 2003b; Pfalz et al., 2009). Similar functions are presumed also for other PPR and TPR-like proteins, specific for various sets of transcripts (Barkan, 2011; Lyska et al., 2013). An example is the PPR10 protein that binds to the 5'- and 3'- regions of chloroplast transcripts of *psaJ-rpl33* or *atpI-atpH*, protecting them from exonucleases both from the 5'- and 3'-directions (Pfalz et al., 2009). Upon binding to the 5'-end of *atpH*, PPR10 promotes its translation by freeing the ribosome binding region from the RNA duplex (Prikryl et al., 2011, Lyska et al., 2013). The loss of PPR-protein leads to the loss of the corresponding mRNA (Schmitz-Linneweber et al., 2005). This mechanism of mRNA protection (and, presumably, control of their level) is unique for plant organelles. It is not clear if a similar mechanism functions in the nucleus.

Editing is a key step in posttranscriptional control of organelle gene expression. It was discovered in mitochondria in 1989 (Covello and Gray, 1989; Gualberto et al., 1989; Hiesel et al., 1989), then in plastids, in 1991 (Hoch et al., 1991). It represents a process of modifying the transcript sequence resulting from the conversion of nucleotide C into U. This leads to the appearance of a sequence distinct from the one encoded by DNA. Editing is reported in all terrestrial plants except liverworts (Rüdinger et al., 2008). In plastids of higher plants, C-U editing is predominant (Takeneka et al., 2013).

One hypothesis is that editing arose initially for correcting genome mutations, which appeared during the plant colonization of the Earth's surface. The result of this correction was to assure the synthesis of a normal protein. Indeed, editing changes often restore the amino acid that is important for protein function (Sugita et al., 2006). The results of editing may be also a new translation initiation codon or, conversely, a stop codon. However, editing also takes place at sites of genome which are not directly associated with the function of the encoded protein (Okuda et al., 2010.): in untranslated RNA regions (5 'and 3' UTR) and in introns. The editing frequency in noncoding regions is very low compared to coding regions. There is speculation with respect to the need for editing for the effectiveness of subsequent splicing (Takenaka et al., 2013).

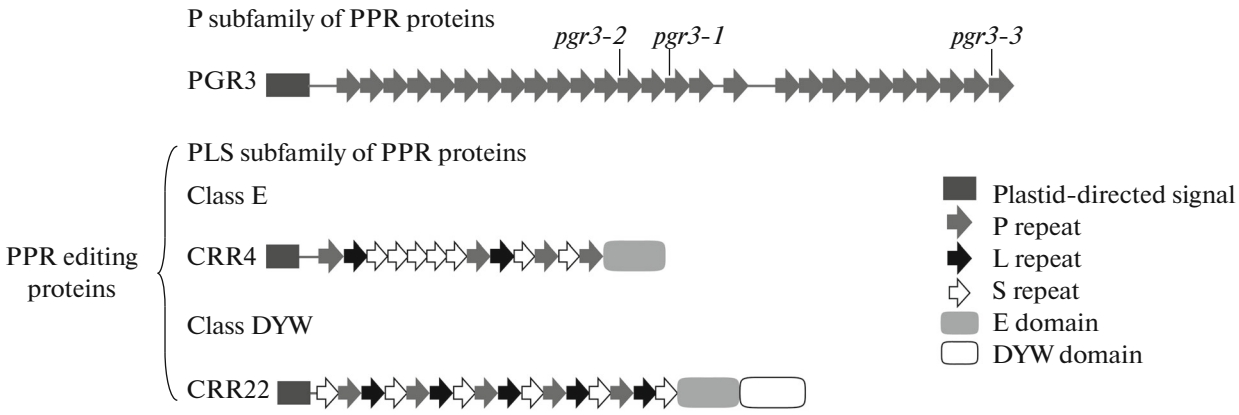
Typically, plastid mRNA in seed plants contain about 30–40 specific editing sites. In arabidopsis 43 editing sites were detected in 18 genes. Thirty-six of these sites reside in coding areas (Ruwe et al., 2013). Monocot and dicot plants differ from each other by more than half of the editing sites (Barkan, 2011).

In mitochondrial genomes, editing sites are considerably more abundant. For example, 441 editing sites were detected in arabidopsis (Giege and Brennicke, 1999), and 491 in rice (Notsu et al., 2002).

Different researchers have repeatedly tried to identify the characteristic features of the RNA sequence at the editing sites (cis-elements) (Bock, Koop, 1997; Miyamoto et al., 2004). It was noted that the RNA sequence of 20–25 nucleotides, located upstream (5') of the editing site contains specific elements required for its recognition (Bock et al., 1996; Chateigner-Boutin et al., 2003; Verbitskiy et al., 2008). Further, a detailed in vitro and in organelle study revealed that nucleotides critically important for editing are located from 5th to 15th positions upstream of the edited C (Takenaka et al., 2013).

Editing transfactors in plants, which recognize the target RNA sequences, are PPR-proteins of the PLS group.

PPR-proteins are subdivided into two large groups: P and PLS proteins (Shikanai, Fujii, 2013). The P group of PPR-proteins is required at different stages of maturation of the RNA transcript. These proteins consist of a canonical 35 amino acid motif (PPR



Scheme of organization of PPR proteins (from Shikanai, 2015).

motif), which is repeated by up to 30 times in tandem (P-region). However, editing involves another group of PPR-proteins, PLS proteins, which are characterized by the presence of three types of repeats: canonical (P), a slightly longer one (L) (of about 36 amino acids), and short (S) (31–34 amino acids) (Small and Peeters, 2000; Lurin et al., 2004; Schmitz-Linneweber and Small, 2008). The C terminus of these proteins contains the E (extended) domain, which is believed to interact directly with the editing enzyme. In about half of the PLS proteins, the E domain is followed by the DYW domain, named for the presence of the highly conserved aspartate-tyrosine-tryptophan (DYW) tripeptide (Fig. 1). It is possible that the DYW domain contributes to the catalytic activity during editing (Manna, 2015).

Each such a protein may be involved in editing 1 to 10 sites. It is even possible that PPR-proteins overlap in their specificity, where a number PPR-proteins may operate at the same editing site. The PPR-proteins involved in editing bind to the RNA reversibly, because mature mRNA must be available for the synthesis of the protein product at the ribosome. RNA binding to PPR-proteins is currently documented for only a few PPR-proteins involved in RNA editing, but more extensively studied and validated for PPR-proteins functioning in the next stage (Okuda et al., 2006; Williams-Carrier et al., 2008).

Recently a new class of proteins was discovered that operates in plant editosomes and is necessary for editing in organelles. These are designated as Multiple Sites Organellar RNA Editing Factors, or MORFs. Each such protein is involved in editing not just one but multiple target sites. Thus, in Arabidopsis, ten members of this family are encoded in the nucleus, two of them operate only in plastids, five operate in mitochondria, and only two operate in both chloroplasts and mitochondria. It was discovered that most editing sites in chloroplast transcripts require the simultaneous operation of both chloroplast MORF proteins (focused to function exclusively in this organelle), as defects in either of the two affect the success and completion of this process (Takenaka et al., 2012; Bentolila et al., 2013). Two MORF proteins form a functional heterodimer, which can be replaced by a homodimer only in some cases. In addition, about 20% of the editing in plastids is controlled by the operation of MORF protein, which functions both in chloroplasts and mitochondria (Bentolila et al., 2013). The function of MORF proteins in hypothetical editosomes is not currently known. It is possible that they represent the link between the PPR-proteins and editing enzymes (Takenaka et al., 2013).

Deamination of cytidine (C) lies at the heart of the editing process in chloroplasts. The reaction that takes place with the C base is similar to the single nucleotide conversion in the uridine biosynthetic pathway carried out by cytidine deaminase, during which the sugar-phosphate backbone of the RNA at the editing site remains intact, while the C nucleotide base is modified. An enzyme catalyzing RNA editing reaction in chloroplasts has not yet been experimentally detected. However, it is believed that it could be (1) a classic cytidine deaminase; (2) a PPR-domain protein with DYW (includes amino acid motif of a classic cytidine deaminase), which provides for cytidine deaminase activity; and (3) an enzyme with modified transaminase activity (Salone et al., 2007; Takenaka et al., 2013).

RNA editing is required for the operation of plant organelles (plastids) and plant survival. Whether editing represents a regulatory mechanism involved in a plant adapting to the changing environmental conditions remains to be determined (Takenaka et al., 2013).

It is believed that editing is the earliest mRNA modification process preceding the emergence of the splicing and restriction of polycistronic transcripts (Freyer et al., 1993; Schmitz-Linneweber and Regel, 2002; Del Campo, 2009). However, intron splicing, the formation of mature mRNA ends, and editing, can

proceed in a different order. For instance, certain sites on the borders of exons are edited only after the splicing of the adjacent introns (Li-Pook-Than and Bonen, 2006).

Splicing is a necessary process of RNA maturation in organelles, in which introns are removed, which otherwise would interrupt the reading frame of genes responsible for plastome photosynthesis and expression. Plant organelles contain two major types of introns: introns of groups I and II, which differ in structure and splicing mechanisms. Twenty of 21 plastid introns in terrestrial plants belong to group II, and only one, in the *trnL-UAA* gene belongs to group I (Cardi et al., 2012). Splicing of each intron is regulated by a number of nuclear-encoded proteins (de Longevialle et al., 2010). Significant progress has been made in identifying these proteins. Sixteen nuclear genes whose products are required for splicing a single or multiple chloroplast introns of group II (Germain et al., 2013) have been detected.

Proteins involved in splicing in chloroplasts are not related to the transcript splicing proteins in the nucleus. Most chloroplast splicing factors contain RNA-binding domains such as CRM, PORR, APO, PPR, and OPR, typical for organelle proteins. The most widely represented are two families of proteins: CRM proteins (Chloroplast RNA splicing and ribosome maturation) operating in several different splice sites; and PPR proteins specific for a single transcript (Schmitz-Linneweber and Small, 2008; Stern et al., 2010). In addition, the splicing of a number of introns of group II involves chloroplast encoded maturase K (the *matK* gene is located in the intron of the *trnK* gene), vital for normal plant development (Rogalski et al., 2006; Legen et al., 2007).

Chloroplasts do not contain spliceosomes similar to nuclear ones. The splicing of introns is a complex process, which includes a large number of factors (proteins). Chloroplast splicing factors interact in different combinations to form complexes with intron RNA, each ensuring the splicing for a certain set of introns (Germain et al., 2013). Splicing is catalyzed by the RNA itself and splicing factors play an accessory role. By binding to the RNA, these factors contribute to its appropriate folding for the formation of a catalytically competent structure.

Undoubtedly, splicing plays a regulatory role during plant development. It can also lead to changes in the relative amounts of mature mRNA in the RNA pool depending on the environmental conditions, thereby, performing an adaptive function (Stern et al., 2010).

The chloroplast genes transcripts level also depends on the rate of degradation. RNA degradation in plastids is regulated by polyadenylation, which, in the nucleus, is involved in mRNA stabilization, but in prokaryotes (and in plastids) is a signal of instability (destruction) (Cardi et al., 2012).

The in vitro and in vivo studies clearly demonstrated that polyadenylation can contribute to RNA degradation in chloroplasts, since the affinity of polynucleotide phosphorylase to polyadenylated RNA is increased. This enzyme is key in the global RNA degradation process in the cell. However, it is not completely clear, to what extent polyadenylation is important for RNA metabolism (turnover) in plastids (Germain et al., 2013).

In chloroplasts, intermediate products of the 3'-end of degradation contain poly(A) tails, which consist not only of adenosine but also of small amounts of other residues, mainly guanosine. It has been shown that polyadenylated transcripts degrade faster than nonadenylated. The molecular mechanisms of RNA degradation in chloroplasts resemble those in bacteria: polyadenylation occurs after endonucleolytic RNA cleavage. The polyadenylated cleavage product is then subjected to prompt exonucleolytic degradation by polynucleotide phosphorylases and, possibly, other exonucleases (Del Campo, 2009). It is not clear whether polynucleotide phosphorylase is the only enzyme involved in polyadenylation in chloroplasts. However, at the moment, it is the only enzyme whose function in polyadenylation is confirmed (Stern et al., 2010).

The observed amounts of polyadenylated transcripts in plastids are extremely small: their detection takes about 50 cycles of PCR (Kudla et al., 1996). In EST databases, polyadenylated RNA are found only occasionally. It is likely that their low incidence reflects their rapid degradation. However, it can also point to the minor role of polyadenylation in the metabolism of chloroplast RNA. These possibilities need to be clarified in the future (Germain et al., 2013).

The processes of transcription and translation in chloroplasts are not strictly linked. There is an additional level of regulation to prevent the initiation of constitutive mRNA translation through the interaction of the Shine-Dalgarno (SD) sequence and 16S ribosomal RNA (SD-16S interaction).

Translation of plastid transcripts takes place at the bacterial-type 70S ribosomes. Chloroplast homologs of bacterial initiation and elongation factors have been identified and some of them have been characterized (Lin et al., 1996; Albrecht et al., 2006; Shen et al., 2013). There is a certain degree of similarity between the translation factors and ribosomal proteins in plastids and bacteria; however, significant differences are also observed (Beligni et al., 2004). Both large and small subunits of the ribosome include in its composition a number of proteins, similar to bacterial proteins, as well as nuclear encoded plastid-specific proteins (PSRPs) (Yamaguchi et al., 2002, 2003; Tiller et al., 2012).

Chloroplast ribosome consists of two subunits, 50S and 30S. Both subunits represent complexes consisting of one or more specific ribosomal RNA and a plu-

rality of proteins. The 30S subunit contains 16S rRNA. The 50S subunit contains 23S, 5S, and 4.5S rRNAs (the smallest one is absent in bacteria; however, it is probably formed by a fragmentation of the 23S rRNA (Tiller and Bock, 2014). The 30S subunit of chloroplast ribosomes contains 24 proteins, three of which are specific to chloroplasts (PSRPs), and 21 proteins are orthologs of *E. coli* 30S ribosomal proteins. The 50S subunit contains 33 proteins: 31 orthologs of bacterial proteins and 2 proteins specific for chloroplasts (PSRPs) (Tiller and Bock, 2014). Ribosomal proteins specific for plastids (PSRP), probably, play a structural role in the plastid ribosome (Sharma et al., 2007).

The initiation of the translation is the most important step in protein production in plastids. A critical step in the initiation of translation is the correct selection, among several possibilities, of the starting codon. The initiation codon in flowering plants is AUG, and less frequently it is GUG (Sugiura et al., 2014). The cis-elements in 5'UTR are an important determinant for the correct initiation and regulation of translation (Staub and Maliga, 1993; Sugiura et al., 2014).

Organization of cis-elements. The peculiarity of translation in chloroplasts is determined by the abundance of the cis-elements (elements of the RNA sequence) in the 5'UTR of chloroplast mRNA. The 5'-UTR regions of plastid transcripts contain SD (Shine-Dalgarno)-like sequences (Sugiura et al., 1998), which function in the initiation of translation through the designation of the correct position for the association of transcripts with ribosomes. The SD elements in the consensus positions are present in approximately one-third of chloroplast genes of land plants. For some of them, the capability to initiate translation has been confirmed. However, most chloroplast genes do not contain a typically located SD sequence, and the binding and/or the arrangement of the translation initiation complex along the mRNA is determined by alternative cis-elements and trans-acting factors (Sugiura et al., 1998; Barkan, 2011; Sugiura, 2014). For instance, in tobacco, the translation of the *rbcL*, *atpE*, and *rps14* transcripts is dependent on SD-like sequences, while the translation of *rps12* and *petB* is partially dependent, and the translation of *psbA* and *atpB* is independent of SD (Lyska et al., 2013).

It has been shown that the translation initiation regions lacking SD sites are less structured than those pocessing SD sequence. Hence, it was suggested that the availability of a start codon is particularly critical in the absence of SD interactions (Tiller and Bock, 2014). The lack of a secondary structure around the start codon appears to contribute favorably to the recognition of the translation starting point and to binding to the 30S subunit of the ribosome. After the starting codon has been designated, the 50S subunit becomes involved in the process, which helps transform the preinitiation complex into an active initiation complex, which then proceeds to elongation steps.

The regulation (adjustment) mechanisms of translation involving cis-elements vary greatly. For instance, a number of alternate cis-elements in 5'UTR plastid transcripts are involved in the initiation of the translation of mRNAs that do not use an SD sequence. However, there is another proposition, that they can complement the SD sequences or provide the specific regulation of the translation in response either to signals at different stages in the organismal development or environmental effects (Peled-Zehavi and Danon, 2007). The SD sequence in the rps2 gene functions as a negative regulator of the translation and also interacts with the trans-acting factors (Plader and Sugiura, 2003).

Cis-regulatory elements have been detected in target regions for transacting factors, in 5'UTR in the *psbC*, *petD*, and *rps7* genes of *Chlamydomonas* (Zerges et al., 1997; 2003; Fargo et al., 1999) and in the mRNA of the tobacco atpB gene (Hirose and Suigura, 2004).

Translation trans-factors are encoded in the nucleus and are generally specific for individual transcripts. They are involved in the initiation of translation through binding with their 5'UTR, which releases ribosome binding sites (Barkan, 2011; Prikryl et al., 2011). These functions are performed by PPR-proteins, such as PPR10, HCF152, CRP1, and PPR38 (gene products of *atpI-atpH*, *psbH-petB*, *petB-petD*, and *clpP-rps12* transcripts, respectively), which were previously identified in arabidopsis, maize, and moss *Physcomitrella patens* (Meierhof et al., 2003; Schmitz-Linneweber et al., 2005; Hattori and Sugita, 2009; Pfalz et al., 2009; Barkan, 2011; Prikryl et al., 2011). Another protein, HCF107 (TPR–protein) found in arabidopsis and maize, regulates the stability and translation of the *psbH* transcript (Stoppel and Meurer, 2013). Recently, a large number of new trans-factors have been described; however, it is still not clear how they interact with the cis-elements.

In chloroplasts, in contrast to prokaryotes, positive regulation of translation predominates. In prokaryotes, the secondary structure of the cis-elements, or a protein bound to mRNA, acts as translation inhibiting factor by blocking access to the initiation site (Gold, 1988; Kozak, 2005; Lyska et al., 2013).

The speed of translation of individual mRNAs has been assumed to be regulated by several mechanisms: (1) a change in the oxidative-reduction potential (redox regulation), which links the translation and photosynthetic electron transport; (2) the autoregulation mechanism connecting the translation and assembly of chloroplast protein complexes (CES is controlling synthesis by epistasy). The CES mechanism is similar to the negative regulation in prokaryotes (Kozak, 2005). The membrane components not included in the complexes (if the membrane components are present in excess) inhibit the initiation of their own translation via 5'UTR. This autoregulation is the main feature of plastids in chlamydomonas; a sim-

Table 4. Summary of published articles on the expression of organelle genomes in plants using macroarray in 2002–2014

Organism	Type of gene set	Experiment	Reference source
Tobacco	PCR products for 118 genes and 11 chloroplast orf	Transplastic tobacco, lacking PEP expression, compared to wild type plant	Legen et al., 2002
	cDNA microarray of 220 PCR probes (71–2373 bp), corresponding to individual genes and intergenic regions	Seedlings were grown in the light/dark, RIP-chip MatK-binding RNA analysis	Nakamura et al., 2003a; Zoschke et al., 2010
Physcomitrella patens	DNA microarray, 108 DNA fragments for detection of all plastid genes	Study of transformants without arginine tRNA	Nakamura et al., 2005
Arabidopsis	cDNA microarray, 79 PCR probes (88–1646 bp) corresponding to protein-coding genes	Effect of *Sig2* gene loss on "total" expression of plastid genes was investigated	Nagashima et al., 2004
Maize (barley as an example of cross-species hybridization)	cDNA microarray, 248 overlapping PCR products (73–1653 bp) corresponding to the entire plastid genome	Identification of RNA associated with PPR proteins in maize (CRP1, PPR 4, PPR5) and whirly in barley (RIP-chip)	Schmitz-Linneweber et al., 2005; Melonek et al., 2010
Chamydomonas reinhardtii	cDNA microarray, PCR products (150–1500 bp) for 47 plastid genes, 9 mitochondrial, and 15 nuclear genes	Study of nonphotosynthetic mutants bearing mutations in a nuclear gene *Mcd1*	Erikson et al., 2005
Cyanidioschyzon merolae	cDNA microarray, 193 PCR probes for protein-coding genes and orf	Role of nuclear-encoded sigma-factors in changing the plastid transcriptome during the dark-light shift	Minoda et al., 2005
	Oligonucleotide microarray of probes to genes of mitochondria, nucleus and chloroplast	Coordination of plastid gene expression in the mitochondria is dynamically modulated by the light and cell cycle in *C. merolae*	Kanesaki et al., 2012
Wheat	Macroarray, 67 PCR probes (200–1259 bp) to 60 plastid genes (without tRNA), and 7 nuclear genes required for plastid function	Germinating seeds, and seedlings at three different stages of development	Siniauskaya et al., 2008
	Macroarray for wheat—PCR products of 28 mitochondrial genes and 5 nuclear genes functionally important for mitochondria were applied to a membrane	Analysis of the "steady-state" transcript levels in the mitochondria, and some nuclear transcripts, at the early stages of wheat seedlings development under normal and stress conditions	Khanam et al., 2007
Corn	DNA microarray, PCR probes to 887 nuclear, 62 chloroplast and 27 mitochondrial genes and orf	Comparison of gene expression in chloro- and etioplasts of maize seedlings at the second leaf stage	Cahoon et al., 2008
Tobacco, potato, tomato	Oligonucleotide microarray, 128 probes (68–71 nucleotides), tobacco chloroplast genes, ycf and orf	Maturation of tomato fruits, chloroplast-chromoplast conversion	Kahlau et al., 2008; Valkov et al., 2009;

Table 4. (Contd.)

Organism	Type of gene set	Experiment	Reference source
Euglena gracilis	Microarray, 96 PCR probes (75–400 bp) for all genes, pseudogenes and orf of euglena	12 different stages of development and effects of stress	Geimer et al., 2009
Arabidopsis	Macroarray, 94 PCR probes to genes of plastid proteins, tRNA and rRNA	Nuclear mutants of arabidopsis with defects in chloroplast function in various growing conditions, and under the influence of various stress factors, data are compared with results of published experiments using Affymetrix 22K ATH1 barley chip	Cho et al., 2009
Cucumber (cross-species hybridization of 9 kinds of different taxa)	Oligonucleotide microarray, 1629 oligonucleotide probes, both regular and "tilling", evenly distributed between coding and noncoding regions	Microarray design is presented, detailed protocol for RNA tagging protocol and subsequent hybridization. Test experiment on cucumber RNA and RNA of other taxa: arabidopsis, tobacco, tomato, spinach, lettuce, alfalfa, lotus, poplar, and barley. This microarray is a great multilateral tool for global functional analysis of the genomes arabidopsis plastids.	Zmienko et al., 2011
Arabidopsis	Oligonucleotide microarray (60 bp probes), sence and antisense probes, entire plastid transcriptome	Analysis of changes in the plastid transcriptome, and in the function of the plant transcription apparatus at the mRNA and protein level during the three stages of seed formation. Results demonstrate how quickly restoration of the plastid transcriptional machinery can occur during imbibition (germination).	Allorent et al., 2013

ilar type of regulation has been already described for the tobacco gene *rbcL* (Wostrikoff and Stern, 2007).

The translational regulation of chloroplast transcripts is type-specific. Thus, it is more specialized than prokaryotes.

It was determined that the translational apparatus of plastids is finely responsive to abiotic stress, particularly, temperature (Xu et al., 2013). The levels of the majority of plastid mRNA remain relatively unchanged under light–darkness conditions; however, the speed of translation dramatically increases during changes in lighting, the development stage, and under the influence of other factors, such as ripening. This is achieved through the function of the plurality of translation transfactors, which contribute to the adaptive modification of the process, primarily, by modulating the plasticity of the chloroplast translation system in response to various effects (Sugiura, 2014).

Apparently, the translational activity of plastids generates a retrograde signal that influences specific aspects of plant anatomy and morphology. However, how this signal is incorporated (when present) in the very complex landscape of the plastid–nuclear relationship is yet to be established (Tiller and Bock, 2014).

The recent decades have been remarkable for the development of high-resolution methods in biology. These methods allow researchers to turn to investigations of complete systems (genomes, transcriptomes, or proteomes) instead of individual genes or pathways. In about a decade, the use of DNA microarrays has become the leading methodology for studies of the total (global) gene expression in plants and animals. A

DNA microarray is multiplex technology used in molecular biology and medicine (Schena et al., 1995; Kehoe et al., 1999; Stoughton, 2005).

The application of genetic chips (microarrays) to studies of genome expression in cell organelles and their interactions with the nucleus is a logical step in the development of this research field. Currently, there are a considerable number of published reports on the studies of organelle genome expression. A short summary on this subject is listed below. As can be seen from Table 4, these are macro- and microarray experiments focused on different problems; in order to resolve them, researchers aim to identify specific genes with the assessment of their functions in a system of interactions between the nucleus and cytoplasm, as well as the effects of these interactions at different stages of the implementation of genetic information in chloroplasts and mitochondria from transcription to translation.

Earlier, research studies at the laboratory of extrachromosomal heredity at IGC NASB created a model collection of the alloplasmatic lines of barley (*Hordeum vulgare* L. ssp. *spontaneum*) with labeled genomes of chloroplasts and mitochondria. The analysis of this collection showed that substitution of a nucleus in various cytoplasmic backgrounds can lead to changes in a number of characteristics of the photosynthetic apparatus: the content of chlorophyll and carotenoids, the number of Q_B-nonreducing PS2 centers, the nonphotochemical quenching of chlorophyll, and others (Shimkevich et al., 2006). To investigate the effects of substitutions on the molecular-genetic level (transcript pool level), a set of DNA probes was developed for the genomes of mitochondria and chloroplasts, which were applied to a membrane to obtain a macroarray (Sinyauskaya et al., 2008; 2012); and on glass, to create a microarray (66 probes to organelle genes and nuclear genes functionally oriented to chloroplasts). A microarray hybridization experiment using these probes was carried out with fluorescently labeled barley cDNA. Using this technology, studies of gene expression profiles were initiated on the mitochondria and chloroplasts of alloplastic barley lines and their euplastic analogs in normal conditions and during periodic temperature stress. It was discovered that the levels of the transcripts of the same gene can change significantly depending on the specific nuclear-cytoplasmic combination both in the norm and during stress. Heat stress generally has a negative effect on the transcript pool by reducing the transcript amounts.

The studies revealed ambiguous differences in the transcript levels of individual PSII genes in chloroplasts and the genes of mitochondrial complexes I and V, between the alloplastic lines of barley and the core grade variety. For some genes, the maximal transcript level was found in the original variety, and for other genes, it was found in the alloplastic lines. Apparently, this is a manifestation of the fact that nuclear-cytoplasmic relationships can modify a plant's response to stress (such as temperature), thereby contributing to its adaptability. These results require further verification and are currently being examined by the RT-PCR and qRT-PCR methods.

Thus, in this review, we attempted to collect and analyze information with respect to the stages of the expression of the plastid genome, demonstrate its multilevel regulation and its relevance, and highlight the interdependence of the processes carried out in different cell compartments.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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