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Review

Chloroplast RNA polymerases: Role in chloroplast biogenesis☆

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ABSTRACT

Plastid genes are transcribed by two types of RNA polymerase in angiosperms: the bacterial type plastid-encoded RNA polymerase (PEP) and one (RPOTp in monocots) or two (RPOTp and RPOTmp in dicots) nuclear-encoded RNA polymerase(s) (NEP). PEP is a bacterial-type multisubunit enzyme composed of core subunits (coded for by the plastid *rpoA*, *rpoB*, *rpoC1* and *rpoC2* genes) and additional protein factors (sigma factors and polymerase associated protein, PAPs) encoded in the nuclear genome. Sigma factors are required by PEP for promoter recognition. Six different sigma factors are used by PEP in *Arabidopsis* plastids. NEP activity is represented by phage-type RNA polymerases. Only one NEP subunit has been identified, which bears the catalytic activity. NEP and PEP use different promoters. Many plastid genes have both PEP and NEP promoters. PEP dominates in the transcription of photosynthesis genes. Intriguingly, *rpoB* belongs to the few genes transcribed exclusively by NEP. Both NEP and PEP are active in non-green plastids and in chloroplasts at all stages of development. The transcriptional activity of NEP and PEP is affected by endogenous and exogenous factors. This article is part of a Special Issue entitled: Chloroplast Biogenesis.

1. Introduction

Compared to their cyanobacterial ancestors, chloroplasts have very small genomes. Typically, the plastid genome (plastome) of embryophytes comprises between 120 and 170 kb. Only 90 to 100 genes have been identified, mostly with functions in photosynthesis or gene expression [1]. In addition to protein-encoding genes and genes for rRNAs and tRNAs a large number of non-coding RNAs (including many antisense RNAs) have recently been detected in plastids [2–9]. Many non-coding plastid RNAs are transcribed from own promoters [8,10]. If these RNAs would be of functional importance, e.g. for the regulation of gene activities [7,11–15], the number of chloroplast genes would increase above 100, but still remain much smaller than the number of genes in any cyanobacterial genome. Nevertheless, the transcriptional apparatus of land plant chloroplasts is more complex than that of bacteria. Bacteria have only one type of RNA polymerase to transcribe all of their genes. Chloroplasts in algae and embryophytes possess a homologous bacterial-type multisubunit enzyme, but angiosperms and possibly the moss *Physcomitrella patens* require in addition one or more single-subunit phage-type RNA polymerases for the transcription of chloroplast genes [16].

Also RNA processing is more complex in chloroplasts than in bacteria [17]. Several primary transcripts contain group I or group II introns and require *cis*- and/or *trans*-splicing. Additionally, C-to-U (in ferns and mosses also U-to-C) editing of the nucleotide sequences is needed for the correct functioning of many chloroplast RNAs in land plants [18]. Not only rRNAs and tRNAs, but also mRNAs are subjected to trimming of their 5′ and/or 3′ ends, a process that is particularly important for the maturation of RNAs transcribed from operons. Like in bacteria, many chloroplast genes are organized in operons and transcribed from one or more promoter(s) into polycistronic RNAs. Chloroplast operons may contain genes belonging to different functional groups, like genes for photosynthesis occurring together with genes encoding ribosomal proteins [1]. Most chloroplast primary polycistronic transcripts are processed into smaller, monocistronic or oligocistronic RNAs before translation [19], facilitating, at the levels of RNA processing, RNA degradation and translation, the control of expression of genes that belong to one and the same operon [17,20,21]. Part of the 3′ ends is protected from RNase digestion by stem-loop structures [22]. Many of the mRNA 5′ and 3′ termini are determined by another mechanism: PPR (pentatricopeptide repeat) proteins bind at specific sites (the later 3′ and 5′ ends) to the freshly transcribed RNAs, thereby protecting them from degradation during the trimming by exonucleases [23,24]. The PPR proteins likely protect their binding sites in the nucleotide sequence since small RNAs representing the PPR protein binding sites are found enriched in chloroplast or leaf RNA, where they contribute to the large number of non-coding chloroplast RNAs mentioned above [24,25].

Differential expression of genes belonging to one and the same operon can also be achieved by using additional promoters within the

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operon [e.g. 8,26,27], which may be accompanied by operon-internal termination of transcription [27]. In *Arabidopsis*, a monocistronic *rbcL* mRNA is generated by termination of transcription between *rbcL* and its downstream neighboring gene *accD*, which is transcribed from own promoters. Termination depends on the RHON1 protein and seems to use an ATP-driven mechanism similar to that of the Rho protein in *Escherichia coli*. In the absence of functional RHON1, a polycistronic mRNA accumulates, comprising the genetic information of *rbcL*, *accD*, *psaI*, *ycf4*, *cemA* and *petA* [27]. Otherwise, the process of termination of transcription in plastids remains obscure. Both transcription and RNA processing seem to take place in the nucleoids where proteins involved in these processes are found together with the plastomic DNA [28,29].

This review focuses on the components of the chloroplast transcriptional machinery and their role during chloroplast biogenesis in angiosperms. Several recent reviews provide more details on the evolution of chloroplast transcription including algae and lower land plants, on plastid sigma factors, RNA polymerase-associated proteins, and on later steps of gene expression in plastids like RNA processing and degradation [16,17,20,22,29–41].

2. Chloroplast RNA polymerases

2.1. The bacterial-type multisubunit RNA polymerase PEP

Chloroplasts have inherited a multisubunit RNA polymerase from their cyanobacterial ancestor. Homologues of the cyanobacterial RNA polymerase core subunits α, β, β′ and β″ are encoded by the *rpoA*, *rpoB*, *rpoC1* and *rpoC2* genes in the plastid genome. Consequently, this enzyme was named plastid-encoded plastid RNA polymerase [PEP; 42]. Like in bacteria, *rpoA*, which encodes the α subunit of PEP, is found in most land plants in a gene cluster together with several genes encoding ribosomal proteins, while *rpoB*, *rpoC1* and *rpoC2*, encoding the β, β′ and β″ subunits, respectively, form a separate operon. The *rpoC* gene coding for the ß′ subunit in other bacteria is split into *rpoC1* and *rpoC2* in cyanobacteria and plastids [43–46]. The PEP β and β′ subunits, but not the α subunit, may functionally substitute the homologous subunits of the *E. coli* RNA polymerase [47,48]. PEP is sensitive to tagetitoxin, an inhibitor of bacterial transcription [49], underpinning the high degree of conservation between the plastid-encoded and eubacterial RNA polymerases. Like the bacterial polymerase, the chloroplast core enzyme requires a sigma (σ) factor for promoter recognition and initiation of transcription [50] (Fig. 1). In contrast to the plastome-encoded core subunits, the chloroplast sigma factors have their genes in the nuclear genome. Land plants and the red algae, *Cyanidium caldarium* and *Cyanidioschyzon merolae*, possess two or more sigma factor genes [51–53]. The green alga *Chlamydomonas reinhardtii*, however, has only one sigma factor [54]. The plant sigma factors belong to the bacterial σ^{70} family [55]. The function of higher plant sigma factors has most intensively been studied in *Arabidopsis*. *Arabidopsis* has six different sigma factors, SIG1–SIG6. Their specific functions in chloroplast transcription have not been completely elucidated yet. However, analyses of knockout mutants have provided first insights (Table 1) for reviews including also information about sigma factors in plants other than *Arabidopsis* [see 38,55–57].

PEP is located in the nucleoids [28–30,39,41], the DNA containing regions of the chloroplasts, and is, independently of its binding to DNA, associated with membranes [73]. PEP can be isolated from plastids as a soluble enzyme, which synthesizes RNA only if DNA is added to the assay [74,75], or as insoluble transcriptionally active chromosome (TAC) [76–78]. The TAC contains the PEP subunits, DNA (used as endogenous template for transcription), RNA, and a large number of other proteins, called pTACs [79, reviewed in 29,30,39,40]. The proteins associated with the core subunits of PEP (the PEP-associated proteins, PAPs) in soluble PEP preparations [80–82] are also identified as components of the larger TAC complex [79] (Fig. 1). Studies on knockout mutants of PAP genes in several labs support the view that the PAPs are required for transcription and its regulation [reviewed in 30,40,41]. Intriguingly, whatever PAP gene was inactivated, the resulting mutant phenotype was very similar: white/ivory leaves, missing or low PEP activity, normal or stimulated transcription of genes transcribed by the nuclear-gene encoded plastid RNA polymerase, NEP, resembling the phenotype of mutants lacking PEP due to knock-out mutagenesis of a chloroplast *rpo* gene. Therefore, Pfalz and Pfannschmidt [30] suggested that, if anyone of the PAPs is lacking, either the generation of the transcriptionally active PEP is interrupted at an early stage of chloroplast development or the intermediate complex is unstable, leading to the observed PEP deficiency. The TAC complex contains proteins in addition to the PAPs, which are supposed to function in gene expression or to have DNA related functions like replication and anchoring the DNA to membranes. Thus, the TAC may be composed of subdomains with different functions [29]. Additional factors involved in transcription, RNA processing and the regulation of gene expression were found in nucleoid preparations [reviewed in 29,30,39–41,83].

2.2. The phage-type RNA polymerase NEP

As the sigma factors, PAPs and pTACs are nuclear-gene encoded, the function of PEP is under nuclear control. Angiosperms (and possibly the moss *P. patens*, [84]) have established an additional layer of nuclear control over plastid gene transcription by the evolution of the nuclear-encoded plastid polymerase, NEP. NEP evolved by duplication(s) of

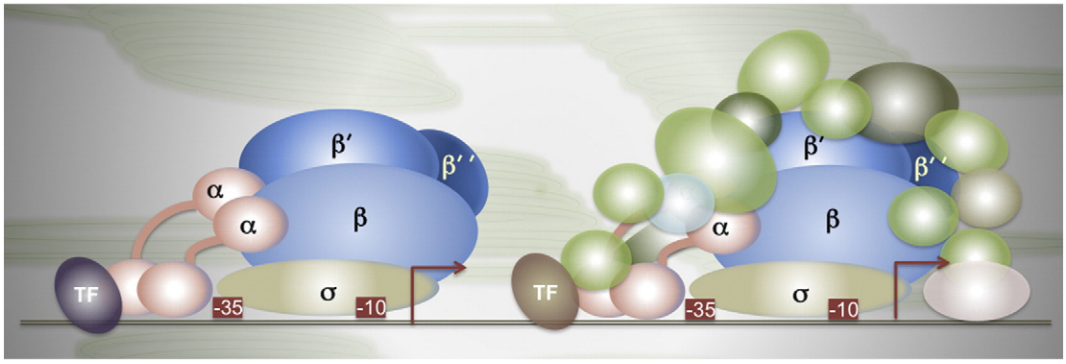

Fig. 1. On the left: PEP is composed of the core subunits α (RpoA), ß (RpoB), ß′ (RpoC1) und ß″ (RpoC2) and a sigma factor (σ). The sigma factor is required for binding to the promoter. Typical PEP promoters have conserved sequence elements at positions −10 and −35 upstream of the site of transcription initiation (arrow). Like their bacterial homologues, the C-terminal domains of the two alpha subunits may interact with DNA and transcription factors, whereas the N-terminal domains may support the assembly of the core subunits. On the right: PEP is associated with numerous additional nuclear-encoded protein factors (PAPs). PAPs have no bacterial homologues. They are essential for PEP activity in chloroplasts. Etioplasts use a less complex PEP, probably similar to the enzyme shown on the left [75,80,82].

Table 1
Function of *Arabidopsis* sigma factors.

Factor	Function	Reference
SIG1	Most abundant sigma factor; accumulates later during leaf development; binds to promoters of photosystem I and II genes; acclimation of photosystem I to changing light qualities; involved in WRKY3-mediated response to biotic stress	[57–61]
SIG2	Transcription of several tRNAs (including *trnE*); transcription of *psaJ*; transcription of *atp* operons; plastid-to-nucleus signaling	[26,62–65]
SIG3	Transcription of *psbN* and *atp* genes; transcription of antisense RNA to *psbT*	[26,66]
SIG4	Transcription of *ndhF*	[67]
SIG5	Stress (osmolarity, temperature, high light) -induced transcription; ABA-induced transcription; transcription of *psbD* from the blue-light-responsive promoter (BLRP); circadian regulation; embryo development	[36,68,69,148,161]
SIG6	Transcription early during chloroplast biogenesis; transcription of *atp* genes; interacts with PPR protein DG1; plastid-to-nucleus signaling	[26,65,70–72]

the nuclear gene encoding the mitochondrial RNA polymerase, which is not a bacterial-type multisubunit polymerase, but an enzyme related to the single-subunit phage-type RNA polymerases [85]. NEP is encoded by the *RPOT* (RNA polymerase of the phage T3/T7 type) gene(s) [86]. The nuclear-gene encoded plastid RNA polymerase is represented by one type (RPOTp; in the basal angiosperm *Nuphar* and in Poacea; other monocots have not been checked) or two (RPOTp and RPOTmp; in eudicots) types of phage-type RNA polymerases. RPOTp is exclusively localized to plastids, whereas RPOTmp is participating in the transcription of plastid and mitochondrial genes [85-91].

Both PEP and NEP are essential for chloroplast transcription. Knockout mutants of PEP show an albino phenotype, lack photosynthesis and can only be grown on sugar-containing medium [e.g.,87,88]. Knocking out the *RPOTp* or *RPOTmp* genes in *Arabidopsis* yields plants with delayed chloroplast biogenesis, altered leaf morphogenesis, and retarded growth (more pronounced in *rpotp* mutants), while *rpotp*/*rpotmp* double mutants exhibit a severe phenotype characterized by chlorophyll deficiency and a complete arrest of growth early in development [see below; 89–91]. The differences between the phenotypes of the single mutants vs. the double mutant indicate partially overlapping functions of RPOTp and RPOTmp in chloroplast gene transcription.

In contrast to the multi-subunit PEP, the phage-type enzymes are composed of only a single catalytic subunit (Fig. 2). The phage T7 RNA polymerase is a genuine single-subunit enzyme; a single protein performs the entire process of transcription from promoter recognition until termination, regardless of whether the DNA template is linear, circular or supercoiled [92]. Similarly, the *Arabidopsis* RNA polymerases RPOTp, RPOTm (the mitochondrial enzyme) and to a lesser extent RPOTmp are able to correctly recognize promoters, transcribe the gene, and stop at a (bacterial) terminator without additional factors in in vitro assays; however, the DNA template has to be in the supercoiled conformation [93]. Yet, if the base sequence of the promoter is altered to prevent base pairing, i.e., if the promoter region is already in a partially open state, the RPOT polymerases are capable of correctly initiating transcription in vitro on linear double-stranded DNA templates (A. Bohne and T. Börner, unpublished data). Most likely, the plant phage-type RNA polymerases need, similar to the related phage-type RNA polymerases in yeast and human mitochondria [94–96], additional factors to melt the DNA duplex at promoter regions *in organello*. Such factors have not been identified in plants [97]. None of the many proteins associated with PEP has been found to interact with NEP. Similar to the high-mobility-group protein TFAM in mammalian mitochondria [96], one or more of the proteins, that bind nonspecifically to DNA and play a role in packaging of chloroplast or mitochondrial DNA might assist in promoter recognition and facilitate the opening of the double helix at the site of transcription initiation by the RPOT polymerases [98] (Fig. 2).

So far studied, PEP and NEP transcribe plastid genes at the same time and in the same tissues (see below). Interactions of both types of RNA polymerases might occur but have not been reported yet. Since plastid DNA is supposed to be exclusively located in nucleoids, NEP should be found, like PEP, in the nucleoid. However, RPOTp and RPOTmp have not been co-purified with PEP and have not been detected in the proteome of plastid nucleoids [28–30,41] most likely because the phage-type polymerases are much less abundant than the PEP subunits. Specific antibodies detect RPOTp and RPOTmp in the stroma and in membrane fractions of plastids. The share of membrane-bound RPOTp and RPOTmp increases during leaf development [99,100, J. Sobanski and T. Börner, unpubl. data]. A RING H2-protein mediates the binding of RPOTmp to the stromal side of the thylakoid membrane in spinach [100]. The way RPOTp binds to the membrane is not known yet.

2.3. NEP and PEP promoters

Three types of NEP promoters have been identified: Type-Ia, Type-Ib, and Type-II (or class Ia, class Ib, class II) [reviewed in 101,107]. Type-Ia NEP promoters are characterized by a conserved YRTa core motif a few nucleotides (nt) upstream of the transcription start site, as found also in plant mitochondrial promoter regions [85] (Fig. 2). The Type-Ib NEP promoters have an additional conserved motif, the GAA-box, about 18

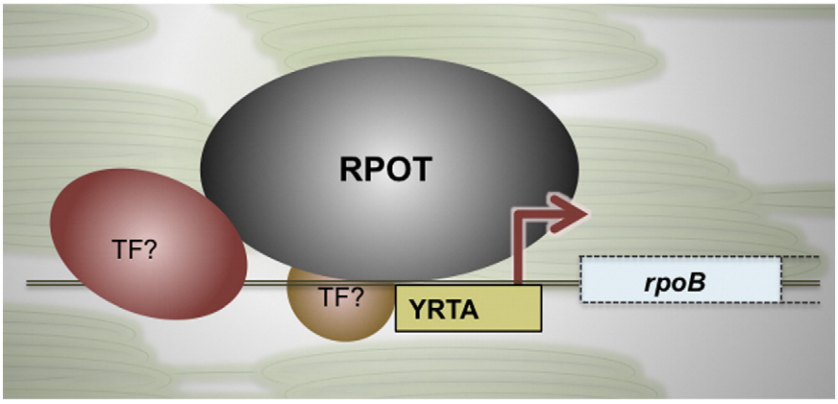

Fig. 2. NEP (RPOTp in monocots, RPOTp and RPOTmp in eudicots) is a phage-type RNA polymerase. NEP may possibly act as a single-subunit enzyme. It is supposed that protein factors (TF) support NEP in promoter recognition. Most NEP promoters have the conserved YRTA motif a few nucleotides upstream of the site of transcription initiation (arrow). The *rpoB* gene enoding the ß subunit of PEP is one of the few genes that are exclusively transcribed by NEP.

to 20 nt upstream of the YRTa motif. Type IIb promoters have been identified in the tobacco plastome; only a few potential Type-IIb promoters have been described in monocots [101]. Experimental data supporting a functional role of the GAA motif exist solely in the case of the Type-IIb promoter of the tobacco *atpB* gene [reviewed in 107]. The GAA sequence has not been detected in a regular distance from the YRTa box in a plastome-wide analysis of transcription in barley plastids suggesting that this promoter type may not be used by NEP in monocots [8]. Type-II comprises all promoters without the YRTa box; also no other consensus motif has been identified near the site of transcription initiation [85]. About 30% of the NEP promoters in barley belong to Type-II [8]. Best investigated are the tobacco *clpP* Type-II promoter, positioned −5 to +25 with respect to the transcription initiation site [102], and the Pc promoter of the *rrn* operon. In spinach, as well as during the early developmental stages of *Arabidopsis* chloroplasts, NEP initiates at the Pc promoter. A transcription factor, CDF2, is involved in the development-dependent regulation of Pc activity in spinach [103,104]. The ribosomal protein RPL4 was co-purified with NEP and CDF2 and suggested to play a role in transcriptional regulation in addition to its function in the ribosome [105].

Many PEP promoters resemble bacterial σ^{70} promoters characterized by −10 and −35 consensus sequence motifs [86,106,107]. However, a number of PEP promoters lack the −10 or the −35 elements, a few even both. In barley chloroplasts, the −10 element (TAtaaT) is located 3–9 nt upstream of the transcription start site; the −35 box (ttGact) is found a further 15–21 nt upstream [8]. Only a few regulatory *cis*-elements and *trans*-factors have been described [reviewed in 107], among them a 22-bp sequence, AAG box, regulating the blue light-, stress-, and ABA-responsive promoter of *psbD* by interaction with PTF1, a positive regulator [108,109], and with SIG5 [68,110,111,148; M. Yamburenko et al., unpubl.]. Mainly changing and modifying the sigma factors might achieve differential transcription of plastid genes by PEP.

A few tRNAs might be transcribed from gene-internal promoters as known from tRNA genes in the nuclear genome. However, such internal promoter elements and the polymerase(s) capable of recognizing them have not been elucidated yet. For a more detailed description of chloroplast promoters and their regulation see [107].

3. The roles of NEP and PEP in different plastid types and during chloroplast biogenesis

3.1. Division of labor between different plastid RNA polymerases

Analyses of plants lacking PEP activity provided insight into the division of labor between PEP and NEP. Hajduckiewicz et al. [42] investigated plastid transcription in a Δ*rpoB* mutant of tobacco and classified plastid genes and operons into those, which are transcribed by PEP (class I), by NEP and PEP (class II) or only by NEP (class III). They proposed, based on the information available at the time, that only PEP transcribes photosystem I and II (*psa* and *psb*) genes, most other genes have both NEP and PEP promoters while NEP alone transcribes a few house-keeping genes (*rpoB*, *accD*, *ycf2*). A recent plastome-wide study on the promoter usage of plastid genes/operons in barley (*Hordeum vulgare* L.) revealed that only *rpoB* (*accD* is a nuclear gene in barley) has exclusively NEP promoters; most other genes were found to be transcribed by NEP in a mutant lacking PEP, i.e. have PEP and NEP promoters, including genes for photosystem I and II proteins and the *rbcL* gene [8]. An active *rbcL* NEP promoter was also observed in *Arabidopsis* leaves [27]. Most of the NEP promoters detected in white, PEP-lacking leaves were inactive in green leaves with PEP activity [8]. Thus, PEP is the predominating RNA polymerase in green leaves. It synthesizes most species of mRNA, transcribes most tRNA genes, and plays a major role in rRNA synthesis. But NEP remains essential in chloroplasts for *rpoB* (forming an operon with *rpoC1* and *C2*), *accD* (in dicots), and participates, in some cases more so than PEP, in the transcription of a number of genes including *clpP*, *atpB*, *atpI*, several genes coding for ribosomal proteins and tRNAs, and, in dicots, *ycf1* and *ycf2* [e.g. 8,42,86,104,112–115].

There exist only a few data supporting the idea that there might also be a division of labor between the two nuclear-gene encoded phage-type polymerases, RPOTp and RPOTmp. Most likely, RPOTp and RPOTmp display their major activities in different tissues and developmental stages. In *Arabidopsis*, the activity of the *RPOTmp* promoter (coupled with GUS) was detected mainly in dividing and young, non-green cells of different organs, whereas the *RPOTp* promoter activity was observed in green, photosynthetically active tissues [116]. Moreover, RPOTmp is targeted to both chloroplasts and mitochondria and the distribution of the enzyme between the two organelles could theoretically be changed by a regulatory mechanism: The RPOTmp mRNA bears two potential start codons for translation. Only the larger protein is dual-targeted to both organelles whereas the shorter protein would be targeted exclusively to mitochondria [117]. Start-codon usage could be controlled via sequences in the 5′ UTR [118], but evidence for this type of regulation is lacking. In addition to the deviating distribution of RPOTp and RPOTmp among different tissues and developmental stages there is some data pointing to different promoter usage by the two polymerases. So far studied, most of the NEP promoters are, however, still active in Δ*rpotp* and Δ*rpotmp* plants indicating that both RPOTp and RpoTmp can recognize most NEP promoters [104,113–115]. Typically, plastid genes/operons have more than one promoter [e.g. 8,68,71,104,113]. RPOTmp transcribes the gene cluster for ribosomal RNA from the so-called Pc promoter (see above) upstream of *rrn16* in *Arabidopsis* immediately after seed imbibition. Using another promoter, PEP is also active in *rrn16* transcription at this early point of development, while at later stages only the PEP promoter becomes responsible for *rrn* transcription [9,104]. RPOTp cannot replace RPOTmp at this site, although it is present in Δ*rpomtp* [104]. Similarly, the strong NEP promoter that drives transcription of the essential *ycf1* gene in wild-type dicot chloroplasts is not used in very young seedlings of Δ*rpotp*, indicating that also RPOTp may play a role at this early stage of development and cannot be substituted by RPOTmp [115].

3.2. NEP and PEP are active during all phases of chloroplast development and in non-green plastid types

3.2.1. Transcription in non-green plastids

Based mainly on the NEP-dependent transcription of the *rpoB* operon and other housekeeping genes and on the role of PEP in the transcription of photosynthesis genes, it was previously hypothesized that NEP would be the principal RNA polymerase activity in non-green tissues and in the early non-green stages of chloroplast development [86]. According to this scenario, only NEP would be active at the beginning of chloroplast biogenesis and be responsible, by transcription of the *rpo* genes and other housekeeping genes, for the appearance of PEP. PEP in turn would transcribe the photosynthesis genes, the activity of which is needed during the greening process and later in the photosynthetically active chloroplasts [119]. These assumptions have not been verified. There is evidence for the presence of PEP and NEP (RPOTp in monocots, RPOTp and RpoTmp in eudicots) at all stages of leaf development and in non-green tissues in roots, seeds, fruits and tubers, though with changing activities; gene expression is distinctly lower in non-green plastids vs. chloroplasts. The activity of both types of RNA polymerases in non-green tissues is not surprising since not only NEP but also PEP transcribes essential housekeeping genes (e.g., tRNA genes). Even transcripts of photosynthesis genes have been observed in non-green plastids [e.g. 8,9,112,120–135].

Arabidopsis roots contain low amounts of the PEP-dependent transcripts *psaA* and *psbA* (and the encoded proteins) as well as the NEP-synthesized *rpoB* mRNA and mRNAs for all sigma factors indicating PEP and NEP activity in wild-type roots [123]. Overexpression of GOLDEN2-LIKE transcription factors (GLKs) leads to chloroplast

development in non-photosynthetic organs. The greening of roots in GLK overexpressors of *Arabidopsis* was accompanied by an increase of many nuclear mRNAs for chloroplast proteins including also the *SIG* transcripts as well as of NEP- and PEP-dependent plastid transcripts [123]. Both NEP and PEP are active in amyloplasts of potato tubers (that never have passed a phase of photosynthetic activity), although the transcriptional activity of all tested genes (proposed to be transcribed by PEP, NEP or both polymerases) is much lower than in chloroplasts [124, also for references for further studies on amyloplasts]. Also red tomato fruits use NEP and PEP to transcribe chromoplast genes, respectively, as deduced from promoter usage [125]. PEP activity might be somewhat more downregulated than NEP activity in red fruits relative to leaves; however, the evidence for this conclusion is weak [125].

3.2.2. Chloroplast biogenesis during seed development and germination

Already dry seeds contain many RNAs transcribed from plastid genes and from nuclear genes encoding chloroplast proteins including several that are involved in photosynthesis [120,127–131]. The levels of several nuclear transcripts for plastid proteins rise quickly after imbibition [129–131], possibly preceding the increase of plastid transcript levels [128]. During seed formation, the embryo of several dicot plants including *Arabidopsis* develops chloroplasts with a specific type of photosynthesis in cotyledons [126], a developmental process accompanied by the expression of most or all chloroplast genes and proposed to be dependent on NEP and PEP activity [132]. These chloroplasts dedifferentiate at the end of seed maturation into the smaller non-green plastids seen in the embryonic tissues of dry seeds. Allorent et al. [127] have studied plastid RNAs and proteins in the different phases of *Arabidopsis* seed formation including dry seeds. Plastid-gene encoded photosynthesis proteins and their mRNAs (presumably PEP-transcribed) were most abundant in the green photosynthetically active chloroplasts and had very low levels in dry seeds, whereas the steady-state levels of (most likely NEP-transcribed) *rpo* mRNAs remained more or less stable during seed development. The (nuclear) transcripts for RPOTp, RPOTmp, SIG2 and SIG4 showed even higher levels in dry seeds than in the preceding steps of seed development. Specific antibodies could also detect comparable amounts of RPOB, RPOTp and RPOTmp in green stages and dry seeds of *Arabidopsis* [120,127], a precondition for the start of transcription in plastids shortly after the start of seed imbibition. Indeed, NEP and PEP polymerases were reported to be not only present but also active during imbibition of the seeds deduced from increasing steady-state levels of plastid RNAs and effects of tagetitoxin, an inhibitor of PEP but not NEP [9,120]. Furthermore, the analysis of promoter usage indicated a much stronger transcription of *rrn16* by PEP compared to NEP (most likely RPOTmp) right from the start of germination [9,104]. Plastid transcripts of many house-keeping genes including *rpoA*, *rpoB*, *rpoC1* and *rpoC2*, and transcripts of several nuclear *SIG and the RPOTp*, *RPOTmp* genes showed enhanced levels already after the 72 h stratification period (4 °C, darkness) [9,120]. At this point of development, PEP and NEP may contribute more or less equally to the transcriptional activity of the plastids. Mustard etioplasts contain a form of soluble PEP (PEP-B), which is built up mainly from the core subunits. After illumination, accessory proteins, the PAPs/pTACs, are added to form the more complex PEP (PEP-A) of chloroplasts [75,80,82] (Fig. 1). PEP-B or a similar form may be active in seeds during stratification. The levels of mRNAs for photosynthesis proteins started to rise shortly after transfer of the seeds to higher temperature and light [9,109]. This should be the phase of chloroplast biogenesis (still in non-green plastids) when PEP becomes the predominating transcriptase in plastids, perhaps accompanied by a transformation of PEP from form B to form A. However, form A could already be present in dry *Arabidopsis* seeds since embryogenesis includes a period with photosynthetically active chloroplasts and expression of several genes encoding pTACs [132].

Clearly, PEP activity increases during chloroplast biogenesis. NEP activity may only shortly increase: early during germination of *Arabidopsis* and rice seeds, a peak of RPOTp expression was observed [127,133] paralleled by higher transcript levels of NEP dependent genes followed by a decrease in NEP activity [127,133,134]. There is, however, no indication for a complete switch from NEP to PEP in plastid gene transcription during the greening process or later in leaf development. NEP remains active, transcribes *rpoB*, *accD* and participates in the transcription of further genes until senescence [122]. It has been found that plastid $tRNA^{Glu}$ binds to and inhibits the activity of RPOTp in vitro [134]. This tRNA is not only involved in translation but plays an additional role in the synthesis of 5-aminolevulinic acid, a chlorophyll and heme precursor. It is massively synthesized by PEP during the greening process. The observed inhibition of NEP by this tRNA in in vitro assays was proposed to reflect a regulatory mechanism, which causes a switch from NEP to PEP transcription during chloroplast biogenesis [134]. Yet, the decreased NEP activity observed at early steps of chloroplast biogenesis seems to be caused by a reduced amount of RPOTp protein [127]. Moreover, the reported inhibition of NEP by $tRNA^{Glu}$ is not specific; also other tRNAs inhibit RPOTp, RPOTmp and even the mitochondrial RNA polymerase RPOTm. If this tRNA effect on phage-type enzymes plays any regulatory role then it might be the inhibition of transcription under conditions of blocked translation with an abundance of tRNAs, but not the suppression of NEP activity during chloroplast biogenesis or leaf development [136].

As described above, the cotyledons of *Arabidopsis* and several other dicots undergo a phase of chloroplast development followed by chloroplast dedifferentiation to small non-green plastids during embryogenesis. The presence of NEP and PEP in dry seeds and at the start of germination is probably not a special case caused by the preceding phase of photosynthetic activity as indicated by the following observation. During the development of true leaves, the biogenesis of chloroplasts starts from proplastids that have never before passed a phase of photosynthetic activity. The existence of NEP or PEP in these proplastids has not been directly shown yet, but NEP and PEP transcripts and the nuclear RPOTp mRNA could be detected in the youngest leaf cells of rice and barley bearing only non-green plastids [133,135].

A massive replication of plastid DNA is observed during chloroplast biogenesis [e.g. 137–139], which most likely is a precondition for the increase in gene expression [140–142]: DNA amount, transcriptional activity, transcript levels and protein synthesis increase during chloroplast biogenesis.

3.2.3. Transcription during leaf development

After germination, the plastid transcriptome profile (analyzed by macroarrays) of *Arabidopsis* seedlings changed during greening of the cotyledons, but remained then relatively stable even if compared with the chloroplast transcriptome of rosette leaves of 3-week-old plants [9]. This is in agreement with the results of a study on transcript levels and transcriptional activities in *Arabidopsis* chloroplasts from cotyledons, young and old leaves [122]. Both PEP and NEP promoters were used at those developmental stages; all investigated genes were more active in young compared to old leaves [122].

A drop in transcription by NEP and PEP after the establishment of the photosynthetic apparatus in chloroplasts is observed in both monocots and dicots and seems to be part of the developmental program [e.g. 122, 139,143,144]. It has recently been proposed that the mutagenic action of reactive oxygen species may damage chloroplast DNA during leaf development to an extent that the genes become non-functional. The transcriptional activity observed at later stages of leaf development would not reflect the synthesis of RNA for gene expression but generate non-coding RNAs involved in posttranscriptional processes and/or transcription-coupled DNA repair [145]. At first glance, this hypothesis is in accord with the observed decrease in transcription during leaf development. However, several facts contradict the assumed presence of non-functional genes and non-functional RNAs in mature chloroplasts. Sequencing analyses of the plastome or the chloroplast transcriptome have never reported a conspicuous accumulation of mutated genes

and transcripts. Chloroplast RNAs show generally sharp bands of identical size in RNA blot hybridizations, regardless of their origin, young or old, dark- or light-grown leaves, which is not expected under the condition of progressing damage of their genes. Moreover, there is still substantial transcriptional activity in old leaves. The transcriptional activity of several chloroplast genes was even higher in one-month-old rosette leaves of 50-day-old *Arabidopsis* plants than in cotyledons of 10-day-old seedlings [122]. Further, it is unlikely that the *psbD* gene encoding the D2 protein of the photosystem II reaction center could somehow escape the proposed mutagenic destruction. This protein has to be continuously synthesized for repair of light-caused damage. This is certainly the reason why *psbD* transcription increases in spite of the decrease in transcription of most other chloroplast genes during leaf development [e.g., 146–148]. Thus, there is evidence for a continuous correct transcription of the chloroplast genes during the whole time span of leaf development.

Also the DNA content remains stable in mature chloroplasts until senescence in *Arabidopsis* and most other investigated plants [122, 139,149,150]. The transcriptional activity, however, may change, under the influence of internal and external factors, though not necessarily accompanied by corresponding changes of RNA and protein levels [discussed in 38,85,151,152]. It has been known since the early studies on gene expression in chloroplasts, that DNA content, transcription, transcript levels and the use of transcripts in translation may be up- and/or downregulated independently of each other [151,152]. Chloroplast transcription is under control of the circadian clock [36,153] and responds to changes in mitochondrial respiration [154]. In particular light effects on plastid transcription have been studied extensively; they play a role in chloroplast biogenesis and during further stages of chloroplast development [reviewed in 85, 119,151,155]. Light, cytokinin and growth at higher temperature stimulate, several stress conditions and the hormones methyl jasmonate (JA), abscisic acid, gibberellic acid and auxin inhibit the transcription of many chloroplast genes in cotyledons and leaves [147,148,156–159] (Fig. 3). The different factors affect chloroplast transcription not independently from each other. For example, abiotic and the (in the context of chloroplast transcription not yet studied) biotic stresses may act via altered hormone levels; light interferes with the action of ABA and cytokinin; hormone effects depend on the age and developmental state of leaves [147,148,159]. It remains to be studied, to which extent these factors control chloroplast biogenesis via transcription of plastid genes and what are the links of the involved signal transduction chains. In part, plastid transcription is controlled via changing amounts of RNA polymerases, i.e. via synthesis and degradation of the enzymes. But stimulation and inhibition of PEP and NEP activities is also involved. Phosphorylation of components of the PEP-dependent transcription machinery has been reported, mainly in the context of effects of a changing redox state [57,58,85,107,155]. Moreover, ppGpp, known as 'alarmone' in bacteria, is active in the stress-induced inhibition of PEP activity [156, 158]. However, nothing is known about the way in which NEP activity is regulated.

4. Concluding remarks

Transcription in plastids is controlled by the nucleus. Although plastids possess genes for the core subunits of a bacterial-type RNA polymerase (PEP), this enzyme can only correctly initiate transcription together with one out of several nuclear-encoded sigma factors. At least in photosynthetically active chloroplasts, PEP is associated with a number of further nuclear-encoded proteins that are also essential for full transcriptional activity and chloroplast biogenesis. In addition, plastid transcription in angiosperms needs a second, fully nuclear-encoded RNA polymerase related to the transcriptases of bacteriophages (NEP). Since NEP transcribes the genes of the PEP core subunits, existence and activity of PEP depend on nuclear genes. Thus, the transcription of plastid genes during chloroplast biogenesis follows a nucleus-controlled developmental program. Two enzymes, RPOTp and RPOTmp, represent NEP activity in eudicots. There is only little information about the division of labor between RPOTp and RPOTmp. NEP and PEP seem to be present and active during all steps of chloroplast biogenesis and in green and non-green tissues. Both PEP and NEP show highest activity during the formation of the photosynthetic machinery. PEP activity increases drastically during the greening process and is the predominating transcriptase in mature chloroplasts. Both PEP and NEP remain active during the entire development of leaves.

Many major questions concerning chloroplast transcription remain unanswered; a few of them are:

Chloroplasts of lower plants including algae with the possible exception of *Physcomitrella* transcribe their genes only by PEP. What advantages do angiosperms have from using a second type of plastid RNA polymerase and eudicots from using even two phage-type enzymes?
What is the role of the many protein factors associated with PEP ("PAPs", "pTACs")?
Which factors help NEP to recognize their promoters? How are promoters recognized that lack detectable consensus sequences?
How are PEP and NEP activated and deactivated?
How can plastid RNA polymerases terminate transcription?

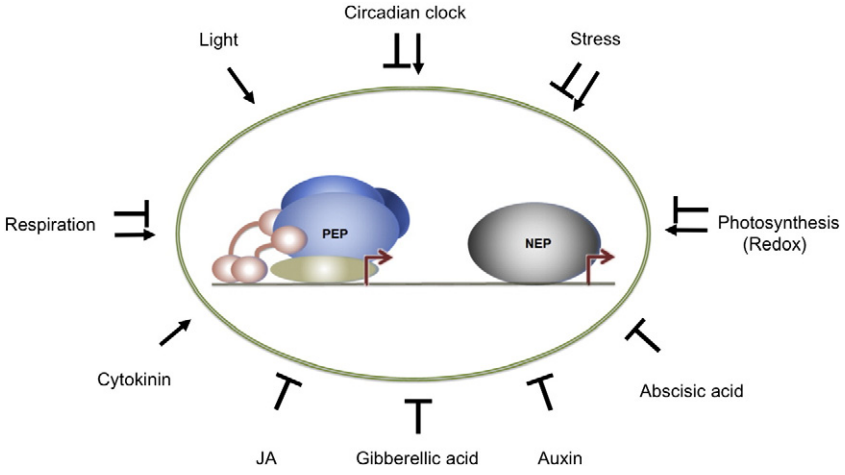

Fig. 3. Endogenous and exogenous factors known to affect transcription in plastids. All factors stimulate (↑) and/or inhibit (T) both PEP and NEP (modified from [85]).

If plastid gene expression is disturbed at early stages of chloroplast biogenesis, the defect is signaled to the nucleus and interrupts chloroplast development by changing the expression pattern of hundreds or even thousands of nuclear genes coding for chloroplast and non-chloroplast proteins [32,65,160]. How does this plastid-to-nucleus signaling operate and how is the complex change in nuclear transcription achieved?

The technical means to answer these questions are available.

Conflict of interest

The authors declare no conflict of interests.

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