Biochimica et Biophysica Acta xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Biochimica et Biophysica Acta

journal homepage: www.elsevier.com/locate/bbabio

Review

Plastid sigma factors: Their individual functions and regulation in transcription☆

Wei Chi *, Baoye He, Juan Mao, Jingjing Jiang, Lixin Zhang

Photosynthesis Research Center, Key Laboratory of Photobiology, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

ARTICLE INFO

Article history:
Received 27 October 2014
Received in revised form 2 January 2015
Accepted 6 January 2015
Available online xxxx

Keywords:
Sigma factor
Plastid
Transcription
Plastid-encoded RNA polymerase

ABSTRACT

Sigma factors are the predominant factors involved in transcription regulation in bacteria. These factors can recruit the core RNA polymerase to promoters with specific DNA sequences and initiate gene transcription. The plastids of higher plants originating from an ancestral cyanobacterial endosymbiont also contain sigma factors that are encoded by a small family of nuclear genes. Although all plastid sigma factors contain sequences conserved in bacterial sigma factors, a considerable number of distinct traits have been acquired during evolution. The present review summarises recent advances concerning the regulation of the structure, function and activity of plastid sigma factors since their discovery nearly 40 years ago. We highlight the specialised roles and overlapping redundant functions of plastid sigma factors according to their promoter selectivity. We also focus on the mechanisms that modulate the activity of sigma factors to optimise plastid function in response to developmental cues and environmental signals. This article is part of a Special Issue entitled: Chloroplast Biogenesis.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

It is generally accepted that the plastids of vascular plants originated from an ancestral cyanobacterial endosymbiont. The plastids have retained bacterial-like gene expression machinery. However, the massive transfer of genes encoding components of the photosynthetic apparatus to the nucleus after endosymbiosis together with the integration of the organelles into plants with distinct developmental stages and cell types has necessitated new strategies to coordinate the expression of plastid and nuclear genes. As a result, eukaryotic features were also acquired after plastids were incorporated into eukaryotic cells [1]. In vascular plant plastids, for example, transcription is carried out by both a nuclear-encoded phage-type RNA polymerase (NEP) and the cyanobacterium-derived plastid-encoded RNA polymerase (PEP) [1,2]. Moreover, most homologues of bacterial transcription factors have been lost in plastids, whereas a number of non-bacterial eukaryotic type nucleic acid binding-proteins likely involved in plastid transcription have been acquired during evolution [3,4]. Therefore, the plastid transcriptional machinery represents a mixed system with prokaryotic and eukaryotic traits [3,4]. It is therefore a good model to study transcription mechanisms in an evolutionary context.

Transcription is roughly divided into the following three major stages: initiation, elongation and termination [5]. Initiation is a dynamic and highly regulated step of gene transcription in both bacteria and eukaryotes. In eubacteria, the key players in transcription initiation are sigma factors (σ), which associate with the catalytic core of RNA polymerase (RNAP) to guide it through the essential steps of initiation, which are promoter recognition and opening and synthesis of the first few nucleotides of the transcript [6]. After RNA synthesis has started, sigma factors are released from the RNAP. However, a population of sigma factors is retained throughout elongation [6]. The PEP has evolved from eubacterial-type RNAPs. Accordingly, sigma factors mediate transcription initiation for PEP. Nevertheless, more complicated mechanisms than those used by eubacteria have evolved to modulate the activity of sigma factors through which plastid transcription is finely regulated.

In past decades, the use of genetic and biochemical approaches together with the ability to manipulate the plastid genome in several species has significantly advanced our understanding of plastid transcription at the mechanistic level. The aim of this review is to summarise recent advances in understanding the structure, function and regulation of the plastid sigma factors. We also pay specific attention to the mechanism through which the activities of sigma factors are modulated to

Abbreviations: ALA, aminolevulinic acid; BLRP, blue-light-responsive *psbD* promoter; CK2, casein kinase 2; CR, conserved region; CSK, chloroplast sensor kinase; MEcPP, methylerythritol cyclodiphosphate; NEP, phage-type RNA polymerase; PAP, 3′-phosphoadenosine 5′-phosphate; PEP, plastid-encoded RNA polymerase; PhANG, photosynthesis-associated nuclear gene; ppGpp, nucleotide guanosine tetraphosphate; PQ, plastoquinone; RNAP, RNA polymerase; UCR, unconserved region

☆ This article is part of a Special Issue entitled: Chloroplast Biogenesis.

* Corresponding author at: Photosynthesis Research Center, Institute of Botany, Chinese Academy of Sciences, Nanxincun 20, Xiangshan, Beijing 100093, China. Tel.: +86 10 62836198; fax: +86 10 82599384.

E-mail address: chiweimr@ibcas.ac.cn (W. Chi).

http://dx.doi.org/10.1016/j.bbabio.2015.01.001
0005-2728/© 2015 Elsevier B.V. All rights reserved.

optimise plastid function in response to developmental cues and environmental signals.

2. Overview of plastid sigma factors

The first report on a plastid sigma factor appeared almost 40 years ago [7]. In this report, a putative plastid sigma factor protein was purified from a green alga, *Chlamydomonas reinhardi*, using biochemical assays. Such proteins with sigma factor activity were subsequently identified in red alga and higher plants [8–12]. Proteins associated with sigma factor activity were initially named "sigma-like" factors [8,9]. Sequence analysis of all cloned plastid sigma factors clearly revealed the presence of the typical sigma factor domains. Together with functional assays, these findings justify their assignment as true sigma factors [12–14]. In contrast to the PEP core subunits, all of the sigma factors from higher plants are nuclear encoded rather than plastid encoded. Bacteria have a single essential housekeeping sigma factor that promotes the transcription of thousands of genes and many alternative sigma factors that promote the transcription of a specialised gene set required for adaptive stress [15]. In agreement with the multiple sigma factors typically found in bacteria, more than one sigma factor is usually found in plastids of higher plants [16–20]. This was also revealed through the sequencing of the genomes of several plastid-containing species including *Arabidopsis* (6 sigma genes), rice (*Oryza sativa*) (6 genes), *Sorghum biocolor* (6 genes), *Vitis vinifera* (6 genes) and *Populus trichocarpa* (7 genes) [21]. In particular, the six *Arabidopsis* sigma factors designated SIG1–SIG6 were extensively studied. Recent work with sigma factor mutants or antisense plants revealed that multiple sigma factors can have specialised roles and overlapping redundant functions based on the promoters they recognise (see below for details).

All plastid sigma factors belong to the superfamily of σ^A/σ^{70} and have sequences homologous to the conserved regions 1.2, 2, 3, and 4 of bacterial sigma factors (Fig. 1). In addition, conserved regions of some plant sigma factors can replace σ^{70} regions of *Escherichia coli* [12]. It was therefore proposed that plastid sigma factors could adopt a similar spatial configuration and perform a function analogous to that of their bacterial homologues. However, plastid factors lack the 1.1 region of bacterial factors [22] (Fig. 1). In addition, plant sigma factors also display considerable variation in conserved domains [22–24]. These changes might confer different affinities for core enzyme, diverse ratios of abortive and processive transcription, and different preferences in choosing sequences of σ^{70}-type promoters to plastid sigma factors compared to those of *E. coli*. Region 2 of SIG5 is one such example. In bacteria, regions 2.1 and 2.2 (two sub-regions of region 2) form the main domain that binds to the RNAP core [25,26]. Regions 2.1 and 2.2 of most plant sigma factors display high similarity to *E. coli* sigma factors except for SIG5, which has the lowest similarity to the common consensus in these two regions. Due to this difference, it has been proposed that the interaction between SIG5 and the core enzyme is weaker than the interactions between core enzyme and other sigma factors. Consequently, SIG5 is less competitive in binding the core, but a holoenzyme comprising SIG5 has a lower level of abortive transcription [22]. Such a property may be critical for stress-inducible trans-factors like SIG5 [27]. For details on the similarities and differences in structure and function between bacterial and plastid sigma factors, we refer readers to the review of Lysenko [22].

The conserved region (CR), which is localised in the C-terminal region of sigma factors, is strikingly uniform in both sequence and length. However, the N-terminal half of the plant sigma factors does not share significant homology with bacterial factors. This region was named the UCR (unconserved region), and its role is only starting to be elucidated [23,24,28]. Schweer et al. identified two regions containing cpCK2 phosphorylation sites in the UCR of SIG6 [29]. One covers the region marked by Ser-94 and Ser-95, while the other spans several serine residues between Ser-174 and Ser-180. Similarly, Thr-170 in the UCR of SIG1 was also demonstrated to be a phosphorylation site [30]. By studying various phosphorylation-site mutants both in planta and in vitro, they demonstrated that the phosphorylation sites within UCR are critical for the activity and specificity of SIG6 [29]. In addition, the UCR of SIG6 was found to be responsible for the interaction of SIG6 with other partners [31]. The UCR function of other plastid sigma factors has not yet been elucidated.

3. Sigma-associated plastid promoters

Although sigma factors do not specifically bind promoters on their own, all specific recognition of promoters by RNAP is mediated by sigma factors [6]. In accordance with the cyanobacterial origin of PEP, despite many variable features, two conserved sequence motifs commonly known as the −35 region (TGACA) and −10 region (TATAAT) of typical bacterial sigma-recognised promoters are found upstream of many plastid genes [32,33]. Because such plastid σ^{70}-type promoters are used by PEP, they are also called PEP promoters. The plastid σ^{70}-type promoter can be fully recognised by *E. coli* RNAP in vitro, suggesting its similarity to the eubacterial σ^{70} promoter [34–36]. It is interesting that the plastid genes of *Chlamydomonas* do not contain valid −35 elements [37], whose function might be served by a more remote sequence in the coding region of some plastid genes of *Chlamydomonas* [38–40].

The function of these elements was dissected by in vitro transcription experiments. Several of these studies were carried on the *psbA*

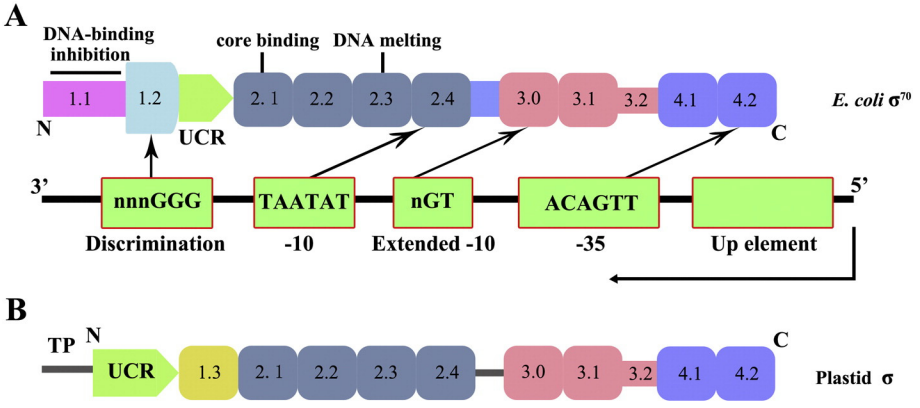

Fig. 1. Structural organisation of sigma factors. (A) Domains and associated functions of *E. coli* σ^{70} proteins. 1.1-4.2 indicate different conserved regions of *E. coli* σ^{70} proteins. UCR indicates an unconserved region. Consensus for the −35 hexamer (−35 to −30), the extension −10 element (−15 to −13), the −10 hexamer −12 to −7), and discriminator DNA (−6 to −1, with an optimal GGG−6 to −4), relative to the transcriptional start are shown in the lower lane. The vertical arrow indicates the transcription initiation site. (B) Structural scheme of plastid sigma factors. TP indicates the transit peptide.

Please cite this article as: W. Chi, et al., Plastid sigma factors: Their individual functions and regulation in transcription, Biochim. Biophys. Acta (2015), http://dx.doi.org/10.1016/j.bbabio.2015.01.001

Download English Version:

https://daneshyari.com/en/article/10795368

Download Persian Version:

https://daneshyari.com/article/10795368

Daneshyari.com