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Circadian regulation of chloroplasts

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Circadian rhythms produce a biological measure of time that increases plant performance. The mechanisms that underlie this increase in productivity require investigation to provide information that will underpin future crop improvement. There is a growing body of evidence that a sophisticated signalling network interconnects the circadian oscillator and chloroplasts. We consider this in the context of circadian signalling to chloroplasts and the relationship between retrograde signalling and circadian regulation. We place circadian signalling to chloroplasts by sigma factors within an evolutionary context. We describe selected recent developments in the integration of light and circadian signals that control chloroplast gene expression.

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Introduction

The Earth rotates on its axis every 24 hours. Life on Earth has adapted to this predictably dynamic environment by evolution of circadian clocks. Plants capture the energy within sunlight in order to power CO_2 fixation. Since this most crucial of resources for plants is available with a predictable cycle, circadian regulation is exceptionally important for plant life. In plants, circadian regulation increases growth and photosynthesis, controls seasonal reproduction, and quantity and quality of seed in model species and crops [1–4]. Therefore, circadian regulation has a substantial impact upon crop and ecosystem productivity. Here, we examine how circadian clocks interact with chloroplasts. This is important, because chloroplasts are the location of photosynthetic light harvesting, CO_2 fixation, and other essential metabolic pathways that sustain agriculture and life on Earth.

Generation of circadian rhythms

Circadian rhythms arise from a network of interconnected genes and proteins that are reviewed in detail elsewhere [5]. Knowledge of network components and architecture is advancing continuously, but one analysis indicates that the *Arabidopsis thaliana* (Arabidopsis) circadian oscillator has three interlocked transcription/translation feedback loops that are connected primarily by repressive feedback [6•,7•,8]. An emergent property is that the abundance or activity of many oscillator components cycle with a period of around 24 hours. Oscillator phase is adjusted to match that of the environment by the process of entrainment. Entrainment occurs by signal-induced alterations in transcription or activity of oscillator components, delaying, advancing or resetting oscillator phase. This includes light signals perceived by the cryptochrome and phytochrome photoreceptors, the blue light-sensing F-box protein ZEITLUPE, photosynthetic sugars, and temperature fluctuations [5,9••].

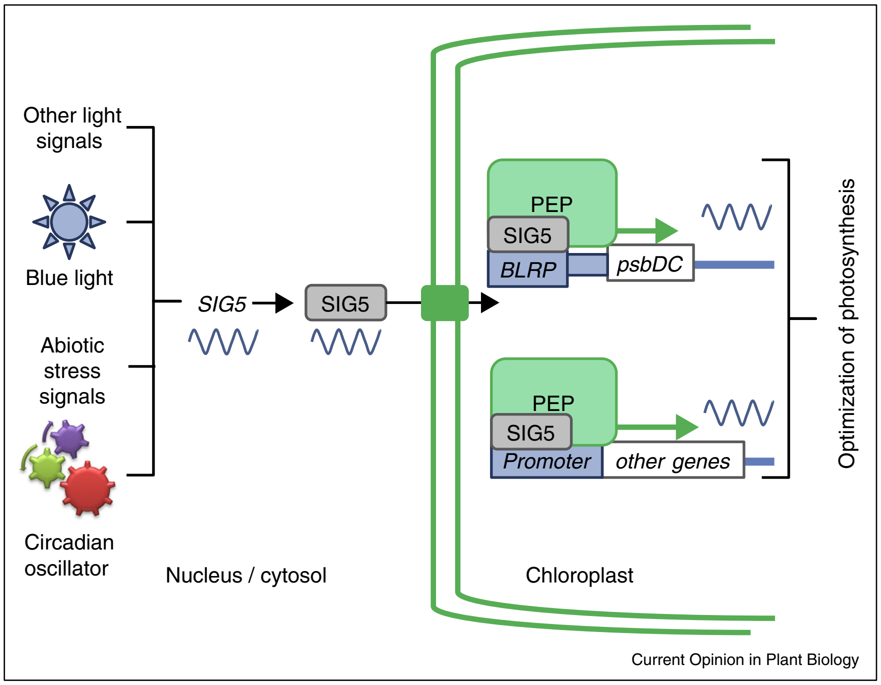
A variety of mechanisms communicate the measure of time generated by the circadian oscillator to circadian-regulated features of the cell. This includes circadian-regulated transcription factors, protein–protein interaction and epigenetic modification. Signalling mechanisms such as Ca^{2+} and cADPR signals, protein phosphorylation, poly(ADP)ribosylation and sugar signalling also contribute to circadian regulation [9••,10–12].

Circadian regulation of chloroplast transcription

The chloroplast genome encodes essential parts of the photosynthetic apparatus, some plastid metabolic proteins, and the plastid transcription/translation system. 70% of chloroplast encoded protein-coding genes can be circadian-regulated in Arabidopsis, depending on experimental conditions [13••]. Rhythmic chloroplast transcripts include components of the photosynthetic apparatus. This is biologically cogent because many nuclear-encoded transcripts that encode components of the photosynthetic apparatus are rhythmic [14], and there are circadian rhythms of photosynthesis [3,15].

Nuclear-encoded regulators of chloroplast transcription couple the eukaryotic circadian clock with chloroplasts. Chloroplast-encoded genes are transcribed by nuclear-encoded plastid RNA polymerase (NEP) and plastid-encoded plastid RNA polymerase (PEP) [16]. NEP is a single-subunit phage type RNA polymerase. PEP is similar to bacterial RNA polymerases in having five core subunits, and requiring a σ^{70}-like sigma factor to confer promoter specificity and initiate transcription [17]. In

Figure 1



Circadian signalling to chloroplasts by a nuclear-encoded sigma factor. Circadian timing information is integrated with abiotic signals to control the abundance of transcripts encoding SIG5. SIG5 enters the plastid and causes oscillations in recruitment of PEP to promoters of a subset of plastid-encoded genes. The leads to rhythmic transcription of certain chloroplast-encoded genes [13••]. In the diagram, genes/transcripts are italic and proteins upright capitals. PEP is the multi-subunit plastid-encoded plastid RNA polymerase. Sine waves indicate components with circadian rhythms. Chloroplast promoters are enclosed in blue boxes; the *psbDC* operon is thought to have four transcription start sites, the most 3′ of which is the SIG5-binding blue light responsive promoter (BLRP) [41].

higher plants, σ^{70}-like sigma factors are encoded by the nuclear genome. During evolution, prokaryotic sigma factor(s) are thought to have transferred from the ancestral chloroplast genome to the eukaryotic nuclear genome, allowing nuclear control of chloroplast gene expression [16]. In Arabidopsis, the nuclear genome encodes six sigma factors (SIGMA FACTOR1 (SIG1)-SIG6).

Nuclear-encoded SIG5 drives circadian rhythms of a subset of chloroplast transcripts (Figure 1) [13••]. SIG5 regulates transcription from an initiation site of the plastid *psbDC* operon called the *psbD* 'blue light responsive promoter' (*psbD* BLRP) [18,19]. In *sig5* loss of function mutants, plastid *psbD* BLRP transcripts become arrhythmic [13••]. Moreover, experimental manipulation of the circadian phase of *SIG5* transcripts causes equivalent alterations in the phase of *psbD* BLRP transcripts [13••]. Interestingly, *SIG5* adjusts the phase of PSII activity, so SIG5 regulation of chloroplast transcription contributes to the circadian timing of photosynthesis [13••]. Therefore, SIG5 communicates circadian timing information from the nuclear-encoded circadian oscillator to the chloroplast genome.

Since circadian signalling by SIG5 accounts for a subset of rhythmic chloroplast transcripts, additional factors likely participate in circadian signalling to chloroplasts. SIG1, SIG3 and SIG4 are good candidates for future study, because these have both rhythmic transcripts and conditionally rhythmic target transcripts on the chloroplast genome [13••]. We suggest additional potential and unexplored mechanisms include post-translational circadian regulation of sigma factor activity, circadian alterations in plastid transcription arising from rhythmic redox signals [20••], circadian regulation by small molecules (e.g., Ca^{2+} or sugar signals [9••,10]), and circadian regulation of plastid transcript or protein turnover.

Evolutionary conservation circadian signalling by sigma factors

Sigma factors participate in circadian signalling in several photosynthetic organisms. In the cyanobacterium *Synechococcus elongatus* PCC7942, the circadian oscillator is evolutionarily distinct from the higher plant oscillator and encoded by *kaiA*, *kaiB* and *kaiC*. However, as in higher plants, sigma factors contribute to the circadian regulation of transcription. Cyanobacterial genomes