Plastids evolved from ancestral cyanobacteria through gradual conversion of an endosymbiont to a plant organelle. Plastids maintained a cyanobacterium-like (eubacterial) transcription machinery. The eubacterial core-enzyme consists of four plastid-encoded subunits (α, β, β′, and β″), and may associate with multiple, nuclear-encoded σ70-type specificity factors. This holo-enzyme is the plastid-encoded plastid RNA polymerase (PEP). The promoters recognized by the PEP are of σ70-type with conserved −10 (TATAAT) and −35 (TTGACA) elements. In addition, species-specific cis-elements and trans-factors regulate psbA, psbD and rrn16 promoter activity. The PEP in chloroplasts associates with up to eight auxiliary proteins. One of them is the plastid transcription kinase (PTK), an enzyme which regulates PEP transcription by σ factor phosphorylation. PTK activity itself is regulated by phosphorylation and the redox state of plastids.

In addition to the eubacterial enzyme, plastids have acquired a second, phage-type RNA polymerase (NEP, nuclear-encoded plastid RNA polymerase). NEP probably evolved by duplication of the mitochondrial transcription machinery. A nuclear gene encodes the NEP catalytic core with a plastid targeting N-terminal sequence. The NEP subunit composition is likely to be similar to the mitochondrial enzyme, which associates...
with at least two specificity factors. NEP recognizes two distinct promoters. Type-I NEP promoters are ~ 15 nt AT-rich region upstream (−14 to +1) of the transcription initiation site (+1) with a conserved YRTA core, a feature shared with plant mitochondrial promoters. Type-II NEP promoters are mainly downstream (−5 to +25) of the transcription initiation site.

There is a division of labor between the two plastid RNA polymerases. Photosynthetic genes and operons have PEP promoters, whereas most non-photosynthetic genes involved in housekeeping functions, such as transcription and translation, have promoters for both RNA polymerases. The NEP promoter(s) of these genes are, with a few exceptions, silent in chloroplasts. Only a few genes are transcribed exclusively from a NEP promoter. One of these is the \textit{rpoB} operon encoding three of the four PEP core subunits. Through transcription of the PEP genes by the NEP the nucleus indirectly controls transcription of plastid genes, thereby integrating the endosymbiont-turned-organelle into the developmental network of multicellular plants.

I. Introduction

The plant cell has three DNA-containing compartments: the nucleus, the mitochondria and the plastids. Plastids evolved from ancestral cyanobacteria through gradual conversion of the endosymbiont to a plant organelle. Although plastids have their own genome and prokaryotic-type gene expression system, they are genetically semi-autonomous and require nuclear gene products for biogenesis and function (Sugiura, 1992; Gray, 1993).

Since the early 1970s, plastid transcription has been extensively studied. Sequence analysis of plastid genomes revealed \textit{rpo} genes encoding homologues of the eubacterial RNA polymerase (RNAP) \( \alpha, \beta \) and \( \beta' \) subunits in the unicellular alga \textit{Euglena gracilis} (Little and Hallick, 1988), and in maize (Hu and Bogorad, 1990, 1991). Biochemical characterization of sigma factor homologues was first accomplished in \textit{Chlamydomonas reinhardtii} (Surzycki and Shellenbarger, 1976), followed by similar work in spinach (Lebs et al., 1983) and mustard (Bülow and Link, 1988). Cloning of the genes for the sigma factors awaited the discovery of PCR (polymerase chain reaction). Homologues of the \textit{E. coli} \( \sigma^{70} \) factor were reported only a few years ago in the red alga \textit{Cyanidium caldarium} (Liu and Troxler, 1996; Tanaka et al., 1996), then in \textit{Arabidopsis thaliana} (Isono et al., 1997b; Tanaka et al., 1997). Promoters for the \textit{E. coli}-like enzyme were first characterized in chloroplast extracts in vitro (Jolly and Bogorad, 1980; Orozco et al., 1985) then in vivo using a transgenic approach (Allison and Maliga, 1995).

The role of a phage-type plastid RNA polymerase in plastid gene transcription has been recognized only recently. The catalytic subunit of the plastid enzyme was fortuitously cloned while searching for the catalytic subunit of the mitochondrial RNA polymerase (Hedtke et al., 1997). Characterization of promoters for the phage-type plastid enzyme was made feasible by plastid transformation, the method used to obtain tobacco plants lacking the \textit{E. coli}-like enzyme by targeted deletion of the plastid \textit{rpo} genes (Allison et al., 1996; Serino and Maliga, 1998). The two plastid RNA polymerases are distinguished by the localization of the genes for their catalytic cores: the \textit{E. coli}-like enzyme is referred to as plastid-encoded plastid RNA polymerase or PEP, whereas the phage-type enzyme is termed NEP for nucleus-encoded plastid RNA polymerase (Hajdukiewicz et al., 1997).

Data on plastid gene transcription were previously viewed as universally applicable from algae to higher plants. As more information accumulates on the plastid transcription machinery, it is becoming increasingly clear that there are significant differences between the plastids of unicellular algae and higher plants. For example \textit{Chlamydomonas reinhardtii}, the model unicellular alga, apparently lacks the phage-type plastid transcription machinery (Rochaix, 1995). Furthermore, there are significant differences between monocots and dicots, or even within dicots, with respect to specific details of transcription. Earlier work on the plastid transcription machinery has been summarized by Bogorad (1991), Igloi and Kössel (1992), Sugiura (1992), Mullet (1993), and Link (1996). For more recent developments see reviews