The Plant

Transcription in eukaryotic cells is controlled by a large number of trans-acting regulatory proteins, most of which recognize cis-acting DNA sequences 5' to the transcription start site. In several cases, it has been demonstrated that expression and specific DNA binding of transcriptional regulators in the context of a developmental program control the temporal and spatial expression of genes. Transcriptional regulators are also part of intracellular signal transduction chains by which cells integrate environmental and physiological cues to change the transcriptional status of genes. As an example, light is one of the most widely studied signals in plants, and several proteins have been identified that bind to regulatory DNA sequences in the promoter regions of light-responsive genes (Gilmartin et al., 1990). The biochemical pathways and the genes downstream of the transcriptional regulators, however, are still largely unknown. The isolation of transcriptional regulators and their genes and the identification of their DNA binding sites are often the important first steps in the genetic, biochemical, and molecular dissection of signal transduction chains. In this respect, plants are no exception, and the efficient transformation systems available for many plants are, in fact, powerful tools that allow the rapid and detailed dissection of regulatory promoter elements.

Two reports in this issue analyze promoter regions for genes that have complex developmental and organ-specific expression patterns. Ohl et al. (pages 837–848) describe the isolation and partial characterization of a gene for phenylalanine ammonia-lyase (PAL) from Arabidopsis. This enzyme catalyzes the first step in the biosynthesis of phenylpropanoids, which are synthesized in response to the plant developmental program, pathogen attack, and UV and mechanical stress. In Arabidopsis, PAL is encoded by a multigene family of comparable size to those from bean, parsley, and rice, supporting the hypothesis that individual PAL genes may encode variant products with distinct functional specializations. Expression of β-glucuronidase activity from the PAL promoter in transgenic Arabidopsis responds to developmental cues, wounding, and light. This expression pattern is similar to the response of the bean PAL promoter in transgenic tobacco (Bevan et al., 1989; Liang et al., 1989) and suggests that regulatory elements within the promoter regions are conserved in a wide range of plants. Consistent with this is the identification in Ohl et al. (pages 837–848) and Lois et al. (1989) of DNA sequence motifs that are conserved in the Arabidopsis and parsley PAL promoter regions and that are present in the promoter regions of other genes for phenylpropanoid pathway enzymes as well.

The gene for 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) in petunia is expressed in different organs at different stages of development. The enzyme catalyzes an essential step in the shikimate pathway and has received much attention as a target for the herbicide glyphosate. Following their initial characterization of the EPSPS gene promoter (Benfey and Chua, 1989), Benfey et al. (pages 849–856) now provide a detailed analysis of 5’ sequences that control the transcription of the EPSPS gene in flowers and seedlings. The highlight of their work is the demonstration of functional redundancy down to the level of cell specificity for two 400-bp to 500-bp DNA fragments that are located approximately 0.8 kb and 1.2 kb 5’ to the transcription start site. As a bonus, they use the EPSPS promoter in combination with the maize A1 gene (for dihydroquercetin 4-reductase) to alter the flower color in two petunia mutant lines unable to accumulate high levels of anthocyanin pigments, further demonstrating the temporal and spatial specificity of this promoter.

At the protein end, transcriptional regulators and DNA-binding proteins are now being identified and isolated at an ever-increasing rate. Based on their DNA binding domains, these factors can be grouped into different classes. Among these are proteins with helix-loop-helix, zinc finger, and leucine zipper motifs in their DNA binding domains. Some of the factors with transcriptional regulatory properties are related to oncoproteins, nuclear hormonal receptors, or homeotic proteins. The recent characterization of the genes for proteins that cause the homeotic leaf phenotype “knotted” in maize (reported by S. Hake at the 32nd Maize Genetics Meeting), and the homeotic flower phenotypes “deficiens” in Antirrhinum majus (Sommer et al., 1990) and “agamous” in Arabidopsis thaliana (Yanofsky et al., 1990) add to this list three potential transcriptional regulators whose correct functions have direct developmental consequences.

Two reports in this issue expand the list of plant transcriptional regulators that belong to the groups of DNA-binding proteins with zinc finger and leucine zipper motifs. Lam et al. (pages 857–866) have isolated the gene for a tobacco nuclear factor, 3AF1, which binds to an AT-rich

Of Fingers, Zippers, and Boxes

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sequence present at the –45 region (Box VI) of the pea rbcS-3A promoter. Box VI, when placed upstream of a truncated cauliflower mosaic virus 35S promoter, functions as a constitutive element that does not respond to light. The protein, encoded by the gene isolated from a tobacco expression library using a Box VI tetramer as the probe, has interesting features, among which are histidines and cysteines in conserved positions relative to other known zinc finger proteins. The conserved amino acids, together with the sensitivity of 3AF1 expressed in Escherichia coli to the metal chelator 1,10-phenanthroline, make 3AF1 a candidate for this class of regulatory DNA-binding proteins.

Singh et al. (pages 891–903) report the isolation and characterization of a maize ocs enhancer binding protein, OCSBF-1, which may be related to the ocs-binding plant factor OCSTF previously identified by Singh et al. (1989) and Tokuhisa et al. (1990). The ocs-element is found in the promoter region of several Agrobacterium T-DNA genes, as well as in the promoter region of certain plant DNA viruses. OCSBF-1 has 2 leucines and a valine in conserved positions adjacent to a basic region. This is typical of a leucine zipper motif, a feature that OCSBF-1 shares with animal and yeast transcriptional regulators such as Jun, Fos, CREB, or GCN4. Recently, Guiltinan et al. (1990) isolated a wheat protein (EMBP-1) that recognizes an abscisic acid response element and that also contains a leucine zipper binding motif. Both OCSBF-1 and EMBP-1 now join the group of previously identified proteins, including the wheat factor HBP-1 (Tabata et al., 1989), the maize factor(s) O2 (Hartings et al., 1989; Schmidt et al., 1990), and the tobacco factors TGA1a and TGA1b (Katagiri et al., 1989), all of which have amino acid homologies in the basic region and part of the leucine zipper motif. These proteins are of particular interest because they may represent a group of plant transcriptional regulators that, similar to the Fos-Jun and ATF-CREB families of proteins, may act by way of conserved DNA binding domains and diverged effector domains. This may allow related transcriptional regulators to act through the same or similar DNA binding sites and provide the cell, based on the different effector domains, with increased flexibility and sensitivity to adjust transcriptional activity in response to a range of biochemical and environmental changes. Clearly, the reports in this issue are part of exciting discoveries to unravel transcriptional regulation in plants.

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