1. INTRODUCTION

The ribosome has attracted our attention not only because of its remarkable ability to polymerize amino acids under the guidance of ribonucleotide triplets, but also because of the relationship between synthesis and assembly of its constituents. In eukaryotes, the ribosome is assembled from four RNA molecules and between 70 and 80 proteins. These various components are distributed over two subunits, one comprising roughly one third and the other two thirds of the total ribosome mass. Accumulation of these components, which may represent as much as 85% of a cell's RNA and 15% of its protein, is an extremely efficient process. How is it that all the macromolecules in such a diverse collection exhibit similar properties of synthesis or accumulation to fulfill the exacting demands of their association? It is becoming increasingly evident that in eukaryotes, posttranscriptional regulatory mechanisms play a role in bringing about and maintaining the appropriate accumulation of ribosomal proteins. Fittingly, regulation of the translation of ribosomal protein messenger RNAs (mRNAs) appears to be one such mechanism. This chapter constitutes a summary of our current
Ribosomal protein gene expression has been studied in systems that fall into two broad groups: early developmental systems and cells in culture. A unique feature of the developmental systems is that rates of ribosome synthesis span extreme values in relatively short periods of time without “outside interference” by the investigator. Rates of ribosome synthesis are “naturally” modulated in differentiating cells. In general, the rate of ribosome synthesis is very high during oogenesis, drops to undetectable levels in early embryos, and then gradually increases during the remainder of embryogenesis. As discussed below, different organisms “adopt different strategies” to regulate ribosomal protein synthesis during this period of extreme variations in demand; for instance, during early embryogenesis, when ribosomal proteins are not needed, \textit{Drosophila} maintains a large store of intact but untranslated ribosomal protein mRNAs, while \textit{Xenopus} selectively degrades these mRNAs. Embryogenesis in \textit{Drosophila} is relatively short; perhaps conservation of the maternal pool of ribosomal protein mRNAs is instrumental for ribosome synthesis later in embryogenesis. The advantage of cultured cells for studies of ribosome synthesis is that they are easily subject to manipulations that produce altered rates of ribosomal synthesis, such as growth rate changes induced by varying nutritional conditions or exposure to different temperatures, hormones, drugs, and growth factors. However, it should be kept in mind that the manipulations that have been used may often be outside the realm of conditions ordinarily experienced by a given cell. Yeast offers a particularly fertile system for investigation of ribosomal protein gene regulation, since it grows naturally under a large variety of thermal and nutritional conditions and also undergoes a natural process of growth arrest (i.e., sporulation). Yeast also offers the facility of introducing wild-type or mutant genes into cells in single or multiple copies (reviewed in Boguslawski\textsuperscript{2}). Genes may be introduced at precisely chosen chromosomal locations or as autonomous elements. This facility can be used to disrupt the balanced production of ribosomal proteins, thereby making apparent a particular regulatory mechanism.

The cloning of ribosomal protein genes has allowed great progress to be made in the understanding of regulation of ribosomal protein gene expression. Table I presents a list of cloned ribosomal protein genes and corresponding references.

2. TRANSLATIONAL REGULATION OF YEAST RIBOSOMAL PROTEIN SYNTHESIS

2.1. Genetics of Yeast Ribosomal Proteins*

The genes for about 20 yeast ribosomal proteins have been cloned (Table I). Curiously, most ribosomal protein gene sequences occur in two (dispersed)