

pairs upstream from the start site. When the activator and  $\sigma^{54}$ -RNA polymerase interact, the DNA between their binding sites forms a loop (see Figure 4-17).

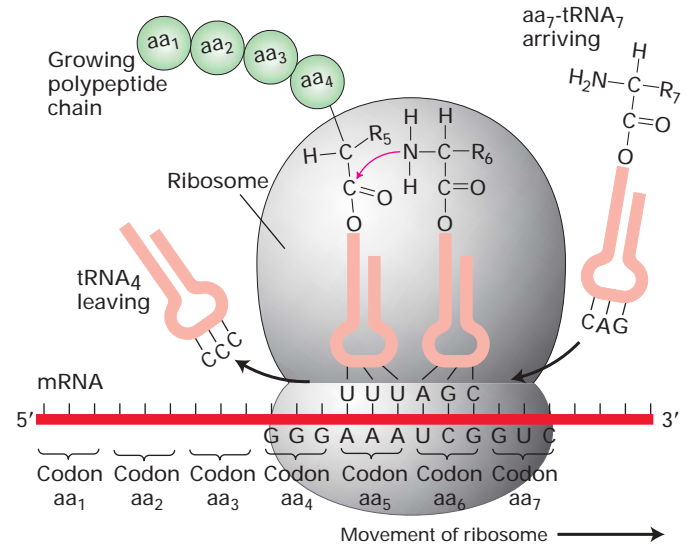
■ In two-component regulatory systems, one protein acts as a sensor, monitoring the level of nutrients or other components in the environment. Under appropriate conditions, the  $\gamma$ -phosphate of an ATP is transferred first to a histidine in the sensor protein and then to an aspartic acid in a second protein, the response regulator. The phosphorylated response regulator then binds to DNA regulatory sequences, thereby stimulating or repressing transcription of specific genes (see Figure 4-18).

## 4.4 The Three Roles of RNA in Translation

Although DNA stores the information for protein synthesis and mRNA conveys the instructions encoded in DNA, most biological activities are carried out by proteins. As we saw in Chapter 3, the linear order of amino acids in each protein determines its three-dimensional structure and activity. For this reason, assembly of amino acids in their correct order, as encoded in DNA, is critical to production of functional proteins and hence the proper functioning of cells and organisms.

Translation is the whole process by which the nucleotide sequence of an mRNA is used to order and to join the amino acids in a polypeptide chain (see Figure 4-1, step 3). In eukaryotic cells, protein synthesis occurs in the cytoplasm, where three types of RNA molecules come together to perform different but cooperative functions (Figure 4-19):

1. **Messenger RNA (mRNA)** carries the genetic information transcribed from DNA in the form of a series of three-nucleotide sequences, called **codons**, each of which specifies a particular amino acid.
2. **Transfer RNA (tRNA)** is the key to deciphering the codons in mRNA. Each type of amino acid has its own subset of tRNAs, which bind the amino acid and carry it to the growing end of a polypeptide chain if the next codon in the mRNA calls for it. The correct tRNA with its attached amino acid is selected at each step because each specific tRNA molecule contains a three-nucleotide sequence, an **anticodon**, that can base-pair with its complementary codon in the mRNA.
3. **Ribosomal RNA (rRNA)** associates with a set of proteins to form **ribosomes**. These complex structures, which physically move along an mRNA molecule, catalyze the assembly of amino acids into polypeptide chains. They also bind tRNAs and various accessory proteins necessary for protein synthesis. Ribosomes are composed of a large and a small subunit, each of which contains its own rRNA molecule or molecules.



▲ **FIGURE 4-19 The three roles of RNA in protein synthesis.** Messenger RNA (mRNA) is translated into protein by the joint action of transfer RNA (tRNA) and the ribosome, which is composed of numerous proteins and two major ribosomal RNA (rRNA) molecules (not shown). Note the base pairing between tRNA anticodons and complementary codons in the mRNA. Formation of a peptide bond between the amino group N on the incoming aa-tRNA and the carboxyl-terminal C on the growing protein chain (purple) is catalyzed by one of the rRNAs. aa = amino acid; R = side group. [Adapted from A. J. F. Griffiths et al., 1999, *Modern Genetic Analysis*, W. H. Freeman and Company.]

These three types of RNA participate in translation in all cells. Indeed, development of three functionally distinct RNAs was probably the molecular key to the origin of life. How the structure of each RNA relates to its specific task is described in this section; how the three types work together, along with required protein factors, to synthesize proteins is detailed in the following section. Since translation is essential for protein synthesis, the two processes commonly are referred to interchangeably. However, the polypeptide chains resulting from translation undergo post-translational folding and often other changes (e.g., chemical modifications, association with other chains) that are required for production of mature, functional proteins (Chapter 3).

### Messenger RNA Carries Information from DNA in a Three-Letter Genetic Code

As noted above, the **genetic code** used by cells is a **triplet** code, with every three-nucleotide sequence, or codon, being “read” from a specified starting point in the mRNA. Of the 64 possible codons in the genetic code, 61 specify individual amino acids and three are stop codons. Table 4-1 shows that most amino acids are encoded by more than one codon. Only two—methionine and tryptophan—have a single