coupled to ATP hydrolysis to ADP (the diphosphate) or AMP (the monophosphate). The coupled reaction can proceed to a much greater extent, since the free-energy change becomes much more negative. In reactions that release energy (for example, oxidation of a sugar), the energy is "captured" and stored by the formation of a phosphate bond in a coupled reaction where ADP is converted into ATP.

In addition to using ATP to store energy, the cell stores and releases hydrogen atoms from biological oxidation-reduction reactions by using nucleotide derivatives. The two most common carriers of reducing power are *nicotinamide adenine dinucleotide* (*NAD*) and *nicotinamide adenine dinucleotide phosphate* (*NADP*).

In addition to this important role in cellular energetics, the nucleotides are important monomers. The polynucleotides (DNA and RNA) are formed by the condensation of nucleotides. The nucleotides are linked together between the $3'$ and $5'$ carbons' successive sugar rings by phosphodiester bonds. The structures of DNA and RNA are illustrated in Fig. 2.16.

DNA is a very large threadlike macromolecule (MW, 2×10^9 D in *E. coli*) and has a double-helical three-dimensional structure. The sequence of bases (purines and pyrimidines) in DNA carries genetic information, whereas sugar and phosphate groups perform a structural role. The base sequence of DNA is written in the $5' \rightarrow 3'$ direction, such as pAGCT. The double-helical structure of DNA is depicted in Fig. 2.17. In this structure, two helical polynucleotide chains are coiled around a common axis to form a double-helical DNA, and the chains run in opposite directions, $5' \rightarrow 3'$ and $3' \rightarrow 5'$. The main features of double-helical DNA structure are as follows:

1. The phosphate and deoxyribose units are on the outer surface, but the bases point toward the chain center. The planes of the bases are perpendicular to the helix axis.
2. The diameter of the helix is 2 nm. The helical structure repeats after ten residues on each chain, at an interval of 3.4 nm.
3. The two chains are held together by hydrogen bonding between pairs of bases. *Adenine is always paired with thymine* (two H bonds); *guanine is always paired with cytosine* (three H bonds). *This feature is essential to the genetic role of DNA.*
4. The sequence of bases along a polynucleotide is not restricted in any way, although each strand must be complementary to the other. The precise sequence of bases carries the genetic information.

The large number of H bonds formed between base pairs provides molecular stabilization. Regeneration of DNA from original DNA segments is known as *DNA replication*. When DNA segments are replicated, one strand of the new DNA segment comes directly from the parent DNA, and the other strand is newly synthesized using the parent DNA segment as a template. Therefore, DNA replication is semiconservative, as depicted in Fig. 2.18. The replication of DNA is discussed in more detail in Chapter 4.

Some cells contain circular DNA segments in cytoplasm that are called *plasmids.*† Plasmids are nonchromosomal, autonomous, self-replicating DNA segments. Plasmids are easily moved in and out of the cells and are often used for genetic engineering. Naturally occurring plasmids can encode factors that protect cells from antibiotics or harmful chemicals.

†Linear rather than circular plasmids can be found in some yeasts and other organisms.