

Measuring Energy Flows in Cedar Bog Lake

In 1936, a young graduate student named Ray Lindeman began his Ph.D. research on a small, marshy pond in Minnesota called Cedar Bog Lake. His pioneering work helped reshape the way ecologists think about the systems they study. At the time, most ecologists were concerned primarily with descriptive histories and classifications of biological communities. A typical lake study might classify the taxonomy and life histories of resident species and describe the lake's stage in development from open water to marsh and then to forest. Blind in one eye, Lindeman couldn't do the microscopy necessary to identify the many species of algae, protozoans, and other aquatic organisms in the lake. Instead, following the ideas of two contemporary English ecologists, Charles Elton and A. G. Tansley, he concentrated on biological communities as systems and looked at broad categories of feeding relationships, for which he coined the term *trophic levels* (from the Greek word for eating). Aided by his wife, Eleanor, Lindeman spent many hours collecting samples of aquatic plants and algae, grazing and predatory zooplankton and fish, and the benthic (bottom-dwelling) worms, insect larvae, crustaceans, and sediment. Back in the laboratory, he measured the plants' photosynthetic rates, the animals' respiration rates, and the total energy content of organic compounds in each of the different trophic levels.

Describing the system in terms of energy flows was a radical departure from ecological methods at the time. Lindeman made a careful balance sheet of the total energy content in the biomass at each trophic level, the energy used in respiration, and the energy content of organic matter deposited in the sediment. To his sur-

prise, he found that each successive feeding level contained only about 10 percent of the energy captured by the level below it. The remainder is lost as heat or deposited in sediments, he argued, because of the work that organisms perform and the inefficiency of biological energy transformations. In his dissertation, Lindeman showed that energy represents a common denominator that allows us to sum up all the processes of production and consumption by the myriad organisms in a biological community.

Lindeman also broke from standard procedure by representing the relationships in his study lake as a mathematical model: He used a series of equations to describe thermodynamic relationships and the efficiency of energy capture and transfer. Ironically, Lindeman's most important paper was rejected by the journal *Ecology* as being too theoretical and too quantitative. It was only after the intercession of G. Evelyn Hutchinson from Yale, with whom Lindeman had a postdoctoral fellowship after finishing his studies at Minnesota, that his mathematical model and energy analysis of Cedar Bog Lake was finally published. Unfortunately, Ray Lindeman died of liver failure before his article appeared. It has since become a landmark in ecological history.

In the years since Lindeman's work, the idea of taking a systemic view of a biological community together with its physical and inorganic environment has become standard in ecology. Energy flows and nutrient cycles are central to the way we understand the workings of ecological systems. Constructing quantitative models to describe, explain, and explore ecological processes has become routine. In this chapter, we will investigate the ways living things use energy and matter and the ways these flows create relationships in ecosystems. (See Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399-418.)

PRINCIPLES OF MATTER AND ENERGY

How and why materials are cycled between the living and nonliving parts of our environment are the domain of **ecology**, the scientific study of relationships between organisms and their environment. Modern biology covers a wide range of scales and themes, from molecules to ecosystems to global systems. Ecology examines the life histories, distribution, and behavior of individual species, as well as the structure and function of natural systems at the level of populations, communities, ecosystems, and landscapes. The systems approach of ecology encourages us to think holistically about interconnections that make whole systems more than just the sum of their individual parts.

In a sense, every organism is a chemical factory that captures matter and energy from its environment and transforms them into structures and processes that make life possible. Therefore, to understand how ecosystems function it is important first to know something of how energy and matter behave—both in the universe and in living things. In this chapter, we will survey some fundamental aspects of energy flow and material recycling within ecosystems.

What Is Matter?

Everything that takes up space and has mass is matter. All matter has three interchangeable physical forms, or phases: gas, liquid, and solid. Water, for example, can exist as a gas (water vapor), a liquid (water), or a solid (ice). Under ordinary circumstances, matter is neither created nor destroyed but is recycled over and over again. The elements in your body have been recycled through many other organisms, over millions of years. Matter is transformed and combined in different ways, but it doesn't disappear; everything goes somewhere. These statements paraphrase the physical principle of **conservation of matter**.

How does this principle apply to human relationships with the biosphere? It implies that, as we use more resources to produce more "disposable" goods, we should pay attention to where our waste products go. What happens to the garbage the truck hauls away? Where does the exhaust from your car go? Ultimately, we need to answer these questions because there is no "away" where we can throw things we don't want any more.

What Is Energy?

Energy and matter are essential constituents of both the universe and living organisms. If **matter** is the material of which things are made, **energy** is the capacity to do work such as moving matter over a distance. Energy can take many different forms. Heat, light, electricity, and chemical energy are common forms. The energy contained in moving objects is called **kinetic energy**. A rock rolling down a hill, the wind blowing through the trees, water flowing over a dam (fig. 2.1), or electrons speeding around the nucleus of an atom are all examples of kinetic energy. **Potential energy** is stored energy that is latent but available for use. A rock poised at the top of a hill contains potential energy, which is converted to kinetic energy when the rock starts rolling down the hill. Chemical energy, stored in the food that you eat and the gasoline that you put into your car, is also potential energy that can be released to do useful work. Energy is often measured in units of heat (calories) or work (joules). One joule (J) is the work done when one kg is accelerated 1 m per second per second ($1 \text{ J} = 1 \text{ kg} \cdot \text{m}^2/\text{s}^2$). One calorie is the amount of energy needed to heat one gram of pure water one degree Celsius. A calorie can also be measured as 4.184 J.

Heat describes the energy that can be transferred between objects of different temperature. When two objects of different temperature are placed in contact, heat transfers to the cooler one until the two reach the same temperature. When a substance absorbs heat, its internal energy increases; the kinetic energy (motion) of its molecules increases, or it may change state: a solid may become liquid, or a liquid become a gas. When you heat a tea kettle on a stove, for example, energy is transferred to the water. We sense the change in heat content as a change in temperature. Some of the water may change state from liquid to vapor. After the

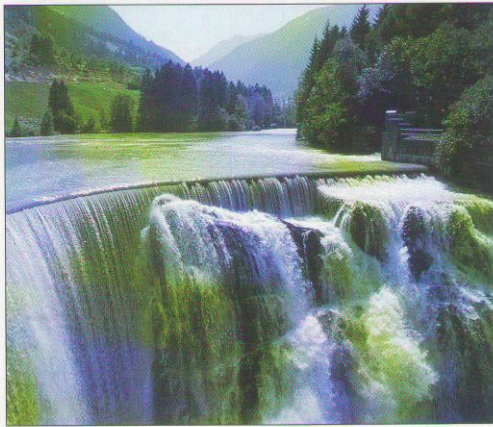


FIGURE 2.1 Water stored behind this dam represents potential energy. Water flowing over the dam has kinetic energy, some of which is converted to heat.

stove is turned off, heat gradually dissipates from the water into the surrounding air. Water requires a relatively large exchange of heat in order to warm or change to steam. One kilogram of iron, for example would warm much faster than one kilogram of water on the same stove. We measure this difference in terms of *specific heat*, the amount of heat required to warm one gram of a substance one degree C. Water requires 4.18 J to warm 1 degree C; a gram of wood takes less than half as much energy (1.7 J), and iron just over one tenth as much energy (0.45 J) to warm 1 degree C.

A substance can have a low temperature but a high heat content, as in the case of a lake that freezes slowly in the fall. Other objects, such as a burning match, have a high temperature but little heat content. Low-quality energy is diffused, dispersed, or low in temperature, so it is difficult to gather and use for productive purposes. Oceans store vast amounts of heat, but converting that heat to useful purposes is difficult. High-quality energy is intense, concentrated, or high in temperature, and it is useful in carrying out work. The intense flames of a very hot fire or high-voltage electrical energy are useful for many purposes. This distinction is important because many of our most common energy sources are low-quality and must be concentrated or transformed into high-quality before they are useful to us.

Why is understanding heat and energy important to understanding environmental science? Because physical characteristics of substances, and their ability to absorb and release energy, control environmental systems. Consider the properties of water, for example. Water's high specific heat keeps lakeshores and seashores relatively cool in the summer and warm in the winter (see "The Miracle of Water," p. 32). Because water absorbs so much heat as it evaporates, atmospheric water vapor redistributes heat around the globe, as well as contributing to the formation of thunderstorms and hurricanes (chapter 9). In addition, the concepts that energy can be converted from work to heat, or from potential to kinetic energy, help explain the ways we store and use energy, both in our bodies and in our electrical utility systems. Further, a common problem in alternative energy production is that alternative energy sources are often more diffuse and difficult to capture than conventional sources such as oil or coal (chapter 12).

Thermodynamics and Energy Transfers

Matter is recycled endlessly through living things, but this recycling is made possible by something that cannot be recycled: energy. Most energy used in ecosystems originates as sunlight. Green plants capture and convert some of this energy to chemical energy, which can be used or stored. Animals consume plants and convert some of the stored chemical energy to kinetic energy and heat. Eventually the energy dissipates and becomes no longer useful. Thus, energy is reused, but it is degraded from higher quality to lower quality forms as it moves through living systems.

Thermodynamics is the study of how energy is transferred, its rates of flow and transformation from one form or quality to another. Thermodynamics is a complex, quantitative discipline, but you don't need a great deal of math to understand some of the broad principles that shape our world and our lives.

The first law of thermodynamics states that energy is conserved: it is neither created nor destroyed under normal conditions. It may be transferred or transformed, but the total amount of energy remains the same.

The second law of thermodynamics states that, with each successive energy transfer or transformation in a system, less energy is available to do work. Even though the total amount of energy remains the same, its intensity and usefulness deteriorates. The second law recognizes the principle known as *entropy*, the tendency of all natural systems to go from a state of order (for example, high-quality energy, such as chemical energy) toward a state of increasing disorder (for example, low-quality energy, such as heat or kinetic energy).

How does the second law of thermodynamics apply to organisms and biological systems? Organisms are highly organized, both structurally and metabolically. Constant care and maintenance is required to keep up this organization, and a constant supply of energy is required to maintain these processes. Every time some energy is used by a cell to do work, some of that energy is dissipated or lost as heat and movement. If cellular energy supplies are interrupted or depleted, the result—sooner or later—is death.

THE BUILDING BLOCKS OF EARTH AND LIFE

Matter consists of elements, which are combined to form molecules and compounds. Each of the 112 known elements has distinct chemical characteristics. Among the more common elements in biology are carbon (C), hydrogen (H), oxygen (O), nitrogen (N), and phosphorus (P) (fig. 2.2, table 2.1).

Atoms, Molecules, and Compounds

An **atom** is the smallest particle that exhibits the characteristics of an element. Atoms are tiny units of matter composed of positively charged *protons*, negatively charged *electrons*, and electrically neutral *neutrons*. Protons and neutrons, which have approximately the same mass, are clustered in the nucleus at the center of the atom (fig. 2.3). Electrons, which are tiny in comparison to protons and neutrons, move at high speed around the nucleus. Atoms that have equal numbers of electrons and protons are electrically neutral. Atoms frequently lose or gain electrons, acquiring a positive or negative electrical charge. Charged atoms are called **ions**. A **cation** has a positive charge (the atom has lost one or more electrons); an

Periodic Table of the Elements

Key

1
Hydrogen
H
1.0079

Atomic number
Name
Symbol
Atomic weight

Metals

Metalloids

Nonmetals

Lanthanides

Actinides

Period	IA		IIA												IIIA	IVA	VA	VIA	VIIA	VIIIA												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18														
1	1 H 1.0079																		2 He 4.0026													
2	3 Li 6.941	4 Be 9.0122											5 B 10.811	6 C 12.0112	7 N 14.0067	8 O 15.9994	9 F 18.9984	10 Ne 20.179														
3	11 Na 22.989	12 Mg 24.305											13 Al 26.9815	14 Si 28.086	15 P 30.9738	16 S 32.064	17 Cl 35.453	18 Ar 39.948														
4	19 K 39.098	20 Ca 40.08	21 Sc 44.956	22 Ti 47.90	23 V 50.942	24 Cr 51.996	25 Mn 54.938	26 Fe 55.847	27 Co 58.933	28 Ni 58.71	29 Cu 63.546	30 Zn 65.38	31 Ga 69.723	32 Ge 72.59	33 As 74.992	34 Se 78.96	35 Br 79.904	36 Kr 83.80														
5	37 Rb 85.468	38 Sr 87.62	39 Y 88.905	40 Zr 91.22	41 Nb 92.906	42 Mo 95.94	43 Tc (99)	44 Ru 101.07	45 Rh 102.905	46 Pd 106.4	47 Ag 107.868	48 Cd 112.40	49 In 114.82	50 Sn 118.69	51 Sb 121.75	52 Te 127.60	53 I 126.904	54 Xe 131.30														
6	55 Cs 132.905	56 Ba 137.34	57 La 138.91	72 Hf 178.49	73 Ta 180.948	74 W 183.85	75 Re 186.2	76 Os 190.2	77 Ir 192.2	78 Pt 195.09	79 Au 196.967	80 Hg 200.59	81 Tl 204.37	82 Pb 207.19	83 Bi 208.980	84 Po (209)	85 At (210)	86 Rn (222)														
7	87 Fr (223)	88 Ra (226)	89 Ac (227)	104 Rf (261)	105 Ha (262)	106 Sg (263)	107 Ns (261)	108 Hs (265)	109 Mt (266)																							
																			58 Ce 140.12	59 Pr 140.907	60 Nd 144.24	61 Pm 144.913	62 Sm 150.35	63 Eu 151.96	64 Gd 157.25	65 Tb 158.925	66 Dy 162.50	67 Ho 164.930	68 Er 167.26	69 Tm 168.934	70 Yb 173.04	71 Lu 174.967
																			90 Th 232.038	91 Pa (231)	92 U 238.03	93 Np (237)	94 Pu 244.064	95 Am (243)	96 Cm (247)	97 Bk (247)	98 Cf 242.058	99 Es (254)	100 Fm 257.095	101 Md 258.10	102 No 259.10	103 Lr 260.105

FIGURE 2.2 The periodic table arranges elements by atomic number (number of protons). The rows and columns are organized to show groups of similar chemical characteristics. For example, the right-most column contains "noble" gases that do not react readily with other elements, and the next column to the left (F, Cl, Br, I, At) includes highly reactive elements known as halogens.

Living things	C, H, O, N
Atmosphere	N, O, Ar, C, Ne, He
Earth, rocks	Fe, O, Si, Mg, Ni, Ca, Al, Na
Economic Metals	Al, Cr, Cu, Fe, Pb, Mn, Ni
Primary toxins	Hg, Pb, Se, Br, Cd, Be, Rn, Ni, As

anion has a negative charge (the original atom gained one or more extra electrons). Some elements tend to lose electrons and form cations readily. Chemically, these elements are known as *metals*. Others tend to gain electrons; these are known as *nonmetals*. A bold line separates the two groups in the periodic table (fig. 2.2), but elements known as *metalloids*, which share some traits of both groups, occur in the table along this line.

We identify atoms by their atomic number, the number of protons in their nuclei. A hydrogen (H) atom has one proton in its nucleus, while a carbon (C) atom has 6. The number of neutrons in atoms of the same element can vary, producing slight variations in atomic mass (the sum of protons and neutrons). Atoms of a single element that differ in atomic mass are *isotopes*. For example, the nuclei of most hydrogen atoms contain only one proton. A small percentage of hydrogen nuclei in nature contain one proton and one neutron. We call this isotope deuterium (^2H). An even smaller percentage of hydrogen atoms have one proton and two neutrons in their nuclei. This isotope is known as tritium (^3H).

Tritium is an example of a radioactive isotope, an unstable form that spontaneously decays by emitting high-energy electromagnetic radiation or subatomic particles, or both. The rate of radioactive decay is indicated by the half-life of an isotope, or the time it takes for half of the atoms to decay. Tritium decays to helium-3 (^3He), with a half-life of 12.5 years. If we started with 1,000 ^3H nuclei, 500 of them would have decayed to ^3He after 12.5 years. Some isotopes of iodine have half-lives measured in seconds, while plutonium, a waste product of nuclear power reactions, has a half-life of 24,000 years. The radioactive emissions from these atoms may be neutrons, beta particles (high-energy electrons), alpha particles (helium nuclei consisting of two protons and two neutrons), positrons (high-energy, positively charged particles), or gamma rays (very short-wavelength radiation). These high-energy emissions can badly damage living cells and tissues. The decades-long debate about storing nuclear waste at Yucca Mountain, Nevada (chapter 12) reflects the danger of radioactive emissions and the long half-life of plutonium.

Because most atoms have some tendency to lose or gain electrons, most are not electrically stable as individuals. They gain stability by joining to form molecules. A **molecule** is a group of atoms, such as O_2 (two oxygen atoms) or H_2O (two hydrogen atoms and one oxygen), that can exist as an individual unit and that has unique properties. We often refer to molecular oxygen (O_2) or molecular nitrogen (N_2), meaning a molecule composed of

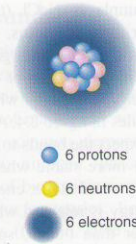


FIGURE 2.5 As difficult as it may be to imagine when you look at a solid object, all matter is composed of tiny, moving particles, separated by space and held together by energy. This model represents a carbon-12 atom, with a nucleus containing six protons and six neutrons; the six electrons are represented as a fuzzy cloud of potential locations, rather than as individual particles.

identical atoms, also called the elemental form of these atoms. A molecule containing different kinds of atoms is called a **compound**. Water (H_2O , fig. 2.4) is a familiar, simple chemical compound. Some compounds are extremely complex. The genetic information in your cells is encoded in molecules called deoxyribonucleic acid (DNA), which contain millions of atoms.

When metals, which tend to give up electrons, combine with nonmetals, which tend to gain electrons, an **ionic compound**

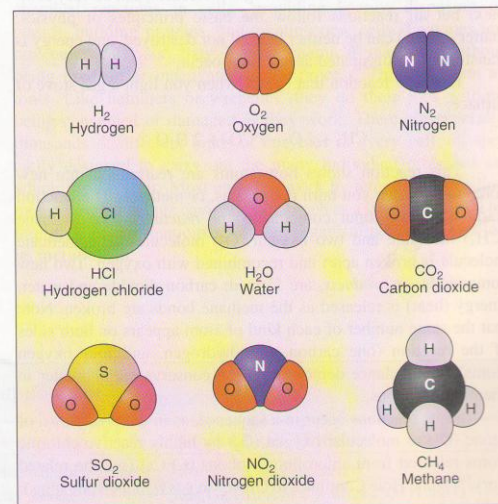


FIGURE 2.4 These common molecules, with atoms held together by covalent bonds, are important components of the atmosphere or important pollutants.

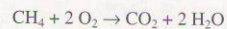
results. A common example is NaCl (table salt). The metal (sodium) releases one or more electrons, becoming a positively charged cation. The nonmetal (chlorine) gains one or more electrons, becoming an anion. When two or more nonmetal atoms join, they do so by sharing electrons in what is called a *covalent bond*. Look at the molecules in figure 2.4. Are the atoms metals or nonmetals? Would you expect the bonds to be ionic or covalent?

Because atoms are more stable when bonded ionically or covalently than when they stand alone, energy is needed to break chemical bonds, and energy is released when bonds are formed. Some bonds are stronger than others, so that more energy is needed to break them, and more energy is released when they are broken. For example, plants require energy from the sun to disrupt the very strong covalent bonds in carbon dioxide (CO₂) and water. Plants use atoms from these compounds to form complex molecules, such as sugars and cellulose. An animal that eats a plant breaks the relatively weak bonds of carbohydrates (sugars and starches), and the resulting atoms recombine to form much stronger bonds of CO₂ and H₂O. The net effect is a release of energy, which powers muscles and allows cells to perform functions such as transferring nutrients and synthesizing proteins.

Chemical Reactions

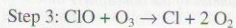
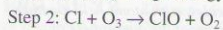
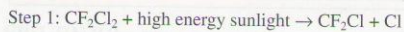
Chemical reactions occur when bonds are broken and re-formed among atoms and compounds. These reactions form the basic compounds on which life depends, and they underlie many of the processes (and problems) in environmental science. Some reactions, such as the breakdown of sugar molecules, can be very complex, but all reactions follow the basic principles of physics: matter (atoms) can be neither created nor destroyed, and energy is transformed or dissipated as reactions occur.

Here is a reaction that occurs when you light a gas stove or furnace:



This reaction shows how atoms are rearranged into new compounds when you burn natural gas, or methane. The reaction starts with two input components, or *reactants*: one methane (CH₄) molecule and two oxygen (O₂) molecules. The methane molecule is broken apart and recombined with oxygen. Two new compounds, or *products*, are formed: carbon dioxide and water. Energy (heat) is released as the methane bonds are broken. Note that the same number of each kind of atom appears on both sides of the reaction (one carbon, four hydrogen, and four oxygen atoms). This balance demonstrates the conservation of matter in chemical reactions.

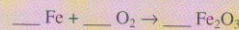
Some reactions occur in a sequence, as in the breakdown of ozone (O₃) to molecular oxygen (O₂) by highly reactive chlorine atoms released from chlorofluorocarbons (CFCs) (see the related story, "Ozone Hole Continues to Grow," at www.mbhe.com/apps):



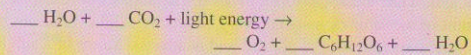
APPLICATION:

Balance a Chemical Equation

In any chemical reaction the same number of atoms of each element must appear on both sides of the arrow. The reaction below represents the net reaction when two reactants, iron and water, combine to produce one product, iron oxide (rust). To balance the equation, first count the number of Fe atoms and O atoms on each side of the arrow. Then fill in the coefficients to make the number of Fe atoms balance. Then fill in the coefficient to make O atoms balance.



Here is a harder example, representing photosynthesis (see fig. 2.11). The reactants water and carbon dioxide are broken apart (with the aid of solar energy) and recombined to produce oxygen molecules, glucose (C₆H₁₂O₆), and water. Again, first count the number of H, C, and O atoms on each side of the equation. Fill in the blanks to balance C, then H, and finally O atoms.



ANSWERS: 4 Fe + 3 O₂ → 2 Fe₂O₃; 12 H₂O + 6 CO₂ + light energy → 6 O₂ + C₆H₁₂O₆ + 6 H₂O

When a molecule or atom loses electrons it is said to be *oxidized*. For example, when iron in the steel body of your car is exposed to oxygen in the air, each iron atom gives up three electrons to the oxygen (O₂) molecules. The formerly blue-black iron becomes a red, iron oxide compound commonly known as rust. In this process, we say that the iron, which lost electrons, was *oxidized*, while the oxygen, which gained electrons, was *reduced*. Not all oxidation-reduction reactions involve oxygen, but many do. Can you think of any other such reactions? What happens when a candle burns?

Acids and Bases

You are probably familiar with **acids**, such as vinegar or battery acid. Mild acids add a sour flavor to foods; strong acids can burn your skin. Chemically, acids are compounds that readily release hydrogen ions (H⁺) in water. Familiar alkaline substances, or **bases**, are also common, especially as cleaning agents: these include baking soda, ammonia, bleach, and drain cleaners. Strong bases are extremely caustic to your skin. Chemically, bases are substances that readily take up H⁺ ions and release hydroxide ions (OH⁻) in solution. The strength of an acid or base solution can be described by its concentration of H⁺ ions, or **pH** (fig. 2.5). Acids have pH values less than 7; they have more H⁺ than OH⁻ ions. Bases have a pH greater than 7; they have more OH⁻ than H⁺ ions. Substances with a pH of exactly 7 are neutral. The pH scale is

logarithmic, which means it increases by factors of 10. A substance with pH 5, therefore, has ten times as many hydrogen ions as one with pH 6. In spring 2002, a train car filled with ammonia (NH₃), the most common nitrogen fertilizer on midwestern farms, overturned in North Dakota. Nearby residents had to be evacuated, because in contact with moisture, ammonia is a strong basic compound that is extremely caustic to living tissue.

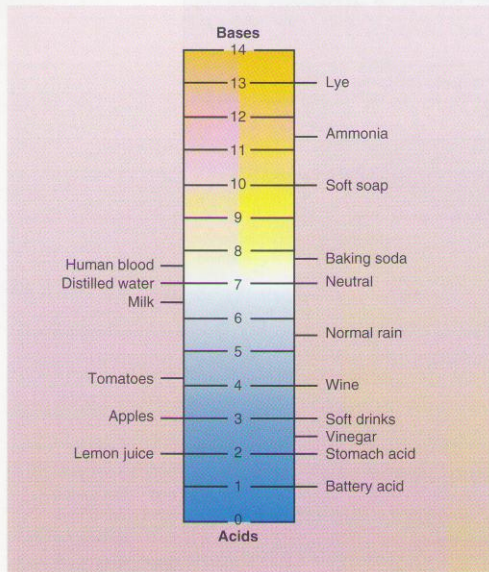


FIGURE 2.5 The pH scale. The numbers represent the negative logarithm of the hydrogen ion concentration in water. Alkaline (basic) solutions have a pH greater than 7. Acids (pH less than 7) have high concentrations of reactive H⁺ ions.

Organic Compounds

Organic compounds, the compounds that make up living things, are large, often complex molecules built on structures of carbon atoms. The carbon atoms can be arranged in chains or rings, or in complex arrangements of many rings and chains. Aside from carbon, some of the most common elements in organic compounds are hydrogen, oxygen, nitrogen, phosphorus, and potassium. There are many types of bioorganic compounds, but they can be grouped into four major categories: lipids, carbohydrates, proteins, and nucleic acids (fig. 2.6, table 2.2). Together these form the structural and functional characteristics of cells.

Cells: The Fundamental Units of Life

All living organisms are composed of cells, minute compartments within which the processes of life are carried out (fig. 2.7). Microscopic organisms, such as bacteria, some algae, and protozoa, are composed of single cells. By contrast, your body contains several trillion cells of about two hundred distinct types. Surrounding every cell is a thin membrane of lipid and protein that receives information and regulates the flow of materials between the cell and its environment. Inside, cells are subdivided into tiny organelles and subcellular particles that provide the machinery for life. Some of these organelles store and release energy. Others manage and distribute information. Still others create the internal structure that gives the cell its shape and allows it to fulfill its functions.

A special class of proteins called enzymes facilitate all the chemical reactions in cells—providing energy, disposing of wastes, building proteins, and creating new cells. Enzymes are molecular catalysts: they initiate chemical reactions without being used up or inactivated in the process. Think of them as tools. Like hammers or wrenches, they do their jobs without being consumed or damaged as they work. There are generally thousands of different kinds of enzymes in every cell, all specially designed to carry out the many individual processes on which life depends. Most enzymes work by temporarily binding molecules in a unique cavity or slot, much as a key fits a lock. The multitude of enzymatic reactions an organism performs is called its **metabolism**.

SUBSTANCE	EXAMPLES	SOME USES	BASIC STRUCTURES
Lipids and hydrocarbons	Fats, oils	Cell membranes, internal cell organelles	Chains of C with attached H
Carbohydrates	Sugars, starches, cellulose	Cell structure, energy storage	Rings or chains of C with attached H and O
Proteins	Muscles, enzymes	Cell structure, function	Chains of amino acids
Nucleic acids	DNA, RNA	Genetic information, protein synthesis	Chains of nucleotides linked by phosphate-sugar bonds