2.3: Energy and Ecosystems

Learning Objectives

After completing this chapter, you will be able to

1. Describe the nature of energy, its various forms, and the laws that govern its transformations.
2. Explain how Earth is a flow-through system for solar energy.
3. Identify the three major components of Earth’s energy budget.
4. Describe energy relationships within ecosystems, including the fixation of solar energy by primary producers and the passage of that fixed energy through other components of the ecosystem.
5. Explain why the trophic structure of ecological productivity is pyramid-shaped and why ecosystems cannot support many top predators.
6. Compare the feeding strategies of humans living a hunting and gathering lifestyle with those of modern urban people.

Introduction

None of planet Earth, its biosphere, or ecosystems at any scale are self-sustaining with respect to energy. In fact, without continuous access to an external source of energy, all of these entities would quickly deplete their quantities of stored energy and would rapidly cool, and in the case of the biosphere and ecosystems, would cease to function in ways that support life. The external source of energy to those systems is solar energy, which is stored mainly as heat and biomass. In effect, solar energy is absorbed by green plants and algae and is utilized to fix carbon dioxide and water into simple sugars through a process known as photosynthesis. This biological fixation of solar energy provides the energetic basis for almost all organisms and ecosystems (the few exceptions are described later). Energy is critical to the
functioning of physical processes throughout the universe, and of ecological processes in the biosphere of Earth. In this chapter we will examine the physical nature of energy, the laws that govern its behaviour and transformations, and its role in ecosystems.

The Nature of Energy

Energy is a fundamental physical entity and is simply defined as the capacity of a body or system to accomplish work. In physics, work is defined as the result of a force being applied over a distance. In all of the following examples of work, energy is transformed and some measurable outcome is achieved:

- A hockey stick strikes a puck, causing it to speed toward a target
- A book is picked up from the floor, lifted, and then laid on a table
- A vehicle is driven along a road
- Heat from a stove is absorbed by water in a kettle, causing it to become hotter and eventually to boil
- The photosynthetic pigment chlorophyll absorbs sunlight, converting the electromagnetic energy into a form that plants and algae can utilize to synthesize sugars

Energy can exist in various states, each of which is fundamentally different from the others. However, under suitable conditions energy in any state can be converted into another one through physical or chemical transformations. The states of energy can be grouped into three categories: electromagnetic, kinetic, and potential.

Electromagnetic Energy

Electromagnetic energy (or electromagnetic radiation) is associated with photons. These have properties of both particles and waves and travel through space at a constant speed of $3 \times 10^8$ m/s (the speed of light). Electromagnetic energy exists as a continuous spectrum of wavelengths, which (ordered from the shortest to longest wavelengths) are known as gamma, X-ray, ultraviolet, visible light, infrared, microwave, and radio (Figure 4.1). The human eye can perceive electromagnetic energy over a range of wavelengths of about 0.4 to 0.7 µm, a part of the spectrum that is referred to as visible radiation or light (1 µm, or 1 micrometre, is $10^{-6}$ m; see Appendix A).

Figure 4.1. The Electromagnetic Spectrum. The spectrum is divided into major regions on the basis of wavelength and is presented on a logarithmic scale ($\log_{10}$) in units of micrometres ($1 \mu m = 10^{-3} mm = 10^{-6} m$). Note the expansion of the visible component and the wavelength ranges for red, orange, yellow, green, blue, and violet colours.

Electromagnetic energy is given off (or radiated) by all objects that have a surface temperature greater than absolute zero (greater than -273°C or 0°K). The surface temperature of a body determines the rate and spectral quality of the radiation it emits. Compared with a cooler body, a hotter one has a much larger rate of emission, and the radiation is dominated by shorter, higher-energy wavelengths. For example, the Sun has an extremely hot surface temperature of about 6000°C, and as a direct consequence most of the radiation it emits is ultraviolet (0.2 to 0.4 µm), visible (0.4 to 0.7...
μm), and near infrared (0.7 to 2 μm). (Note that the interior of the Sun is much hotter than 6000°C, but it is the surface temperature that directly influences the emitted radiation.) Because the surface temperature of Earth averages much cooler at about 15°C, it radiates much smaller amounts of energy at longer wavelengths (peaking at a wavelength of about 10 μm).

Image 4.1. The energy of the Sun is derived from nuclear fusion reactions involving hydrogen nuclei. These reactions generate enormous quantities of thermal and electromagnetic energy. Solar electromagnetic radiation is the most crucial source of energy that sustains ecological and biological processes. Source: NASA image: [http://sdo.gsfc.nasa.gov/assets/img/latest/latest_4096_0304.jpg](http://sdo.gsfc.nasa.gov/assets/img/latest/latest_4096_0304.jpg)

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**Kinetic Energy**

Kinetic energy is associated with bodies that are in motion. Two classes of kinetic energy can be distinguished.

**Mechanical kinetic energy** is associated with any object that is in motion, meaning it is travelling from one place to another. For example, a hockey puck flying through the air, a trail-bike being ridden along a path, a deer running through a forest, water flowing in a stream, or a planet moving through space are all expressions of this kind of kinetic energy. The amount of mechanical kinetic energy is determined by the mass of an object and its speed.

**Thermal kinetic energy** is associated with the rate that atoms or molecules are vibrating. Such vibrations are frozen at -273°C (absolute zero), but are progressively more vigorous at higher temperatures, corresponding to a larger content of thermal kinetic energy, which is also referred to as heat.

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**Potential Energy**

Potential energy is the stored ability to perform work. To actually perform work, potential energy must be transformed into electromagnetic or kinetic energy. There are a number of kinds of potential energy:
Gravitational potential energy results from gravity, or the attractive forces that exist among all objects. For example, water stored at any height above sea level contains gravitational potential energy. This can be converted into kinetic energy if there is a pathway that allows the water to flow downhill. Gravitational potential energy can be converted into electrical energy through the technology of hydroelectric power plants.

Chemical potential energy is stored in the bonds between atoms within molecules. Chemical potential energy can be liberated by exothermic reactions (those which lead to a net release of thermal energy), as in the following examples:

- Chemical potential energy is stored in the molecular bonds of sulphide minerals, such as iron sulphide (FeS₂), and some of this energy is released when the sulphides are oxidized. Specialized bacteria can metabolically tap the potential energy of sulphides to support their own productivity, through a process known as chemosynthesis (this is further examined later in this chapter).
- The ionic bonds of salts also store chemical potential energy. For example, when sodium chloride (table salt, NaCl) is dissolved in water, ionic potential energy is released as heat, which slightly increases the water temperature.
- Hydrocarbons store energy in the bonds between their hydrogen and carbon atoms (hydrocarbons contain only these atoms). The chemical potential energy of gasoline, a mixture of liquid hydrocarbons, is liberated in an internal combustion engine and becomes mechanically transformed to achieve the kinetic energy of vehicular motion.
- Organic compounds (biochemicals) produced metabolically by organisms also store large quantities of potential energy in their inter-atomic bonds. The typical energy density of carbohydrates is about 16.8 kJ/g, while that of proteins is 21.0 kJ/g, and lipids (or fats) 38.5 kJ/g. Many organisms store their energy reserves as fat because these biochemicals have such a high energy density.

Electrical potential energy results from differences in the quantity of electrons, which are subatomic, negatively charged particles that flow from areas of high density to areas where it is lower. When an electrical switch is used to complete a circuit connecting two areas with different electrical potentials, electrons flow along the electron gradient. The electric energy may then be transformed into uses as light, heat, or work performed by a machine. A difference in electrical potential is known as voltage, and the current of electrons must flow through a conducting material, such as a metal.

Elasticity is a kind of potential energy that is inherent in the physical qualities of certain flexible materials and that can perform work when released, as occurs when a drawn bow is used to shoot an arrow.

Compressed gases also store potential energy, which can do work if expansion is allowed to occur. This type of potential energy is present in a cylinder containing compressed or liquefied gas.

Nuclear potential energy results from the extremely strong binding forces that exist within atoms. This is by far the densest form of energy. Huge quantities of electromagnetic and kinetic energy are liberated when nuclear reactions convert matter into energy. A fission reaction involved the splitting of isotopes of certain heavy atoms, such as uranium-235 and plutonium-239 (U²³⁵ and ²³⁹P), to generate smaller atoms plus enormous amounts of energy. Fission reactions occur in nuclear explosions and, under controlled conditions, in nuclear reactors used to generate electricity. A fusion reaction involves the combining of certain light elements, such as hydrogen, to form heavier atoms under conditions of extremely high temperature and pressure, while liberating huge quantities of energy. Fusion reactions involving hydrogen occur in stars and are responsible for the unimaginably large amounts of energy that these celestial bodies generate and radiate into space. It is thought that all heavy atoms in the universe were produced by fusion reactions occurring in stars (see Chapter 3). Fusion reactions also occur in a type of nuclear explosive device known as a hydrogen bomb. A technology has not yet been developed to exploit controlled fusion reactions to generate electricity;
if and when available, controlled fusion could be used to generate virtually unlimited amounts of commercial energy (see Chapter 13).

Image 4.2. Organic matter and fossil fuels contain potential chemical energy, which is released during combustion to generate heat and electromagnetic radiation. This forest fire was ignited by lightning and burned the organic matter of a pine forest. Source: NASA image: Kari Greer, http://www.nasa.gov/images/content/710937main_climate-fire-lg.jpg

Units of Energy

Although energy can exist in various forms, all of them can be measured in the same or equivalent units. The internationally accepted system for scientific units is the SI system (Système International d'Unités), and its recommended unit for energy is the joule (J). One joule is defined as the energy required to accelerate 1 kg of mass at 1 m/s² (1 metre per second per second) over a distance of 1 m.

A calorie (or gram-calorie, abbreviation cal) is another unit of energy. One calorie is equivalent to 4.184 J, and it is defined as the amount of energy required to raise the temperature of 1 g of pure water by 1°C (specifically, from 15°C to 16°C). Note, however, that the dietician’s “Calorie” is equivalent to 1000 calories (1 Calorie = 1 kcal). However, the energy content of many food products is now listed in kJ in countries using the SI system of units, such as Canada.

Energy Transformations

As was previously noted, energy can be transformed among its various states. For example, when solar electromagnetic radiation is absorbed by a dark object, it is transformed into thermal energy and the absorbing body increases in temperature. The gravitational potential energy of water stored at a height is converted into the kinetic energy of flowing water at a waterfall, which may be harnessed using hydroelectric technology to spin a turbine and generate electrical energy. As well, visible wavelengths of solar radiation are absorbed by chlorophyll, a green pigment in plant foliage, and some of the captured energy is converted into chemical potential energy of sugars via the biochemistry of photosynthesis.
All transformations of energy must behave according to certain physical principles, which are known as the laws of thermodynamics. These are universal principles, meaning they are always true, regardless of the circumstances.

### The First Law of Thermodynamics

The first law of thermodynamics, also known as the law of conservation of energy, can be stated as follows: Energy can undergo transformations among its various states but it is never created or destroyed; therefore, the energy content of the universe remains constant. A consequence of this law is that there is always a zero balance among the energy inputs to a system, any net storage within it, and the energy output from the system.

Consider the case of an automobile driving along a highway. The vehicle consumes gasoline, an energy input that can be measured. The potential energy of the fuel is converted into various other kinds of energy, including kinetic energy embodied in forward motion of the vehicle, electrical energy powering the lights and windshield wipers, heat from friction between the vehicle and the atmosphere and road surface, and hot exhaust gases (thermal energy) and unburned fuel (chemical potential energy) that are vented through the tailpipe. Overall, in accordance with the first law of thermodynamics, an accurate measuring of all of these transformations would find that, while the energy of the gasoline was converted into various other forms, the total amount of energy was conserved (it remained constant).

### The Second Law of Thermodynamics

The second law of thermodynamics can be expressed as follows: Transformations of energy can occur spontaneously only under conditions in which there is an increase in the entropy of the universe. Entropy is a physical attribute related to disorder, and is associated with the degree of randomness in the distributions of matter and energy. As the randomness (disorder) increases, so does entropy. A decrease in disorder is referred to as negative entropy. Consider, for example, an inflated balloon. Because of the potential energy of its compressed gases, that balloon may slowly leak its contents to the surrounding atmosphere, and it may even burst. Either of these outcomes can occur in a spontaneously fashion, because both processes would represent an increase in the entropy of the universe. This is because compressed gases are more highly ordered than those widely dispersed in the atmosphere. In contrast, dispersed gases in the atmosphere would never spontaneously relocate to inflate a balloon. A balloon will only inflate only if energy is expended through a local application of work, such as by a person blowing into the balloon. In other words, energy must be expended to cause a local decrease of entropy in a system. However, note that this energy cost itself gives rise to an increase in the entropy of the universe. For instance, the effort of a person inflating a balloon involves additional respiration, which uses biochemical energy and results in heat being released into the environment.

Another example concerns planet Earth. The planet continuously receives solar radiation, almost all of which is visible and near-infrared wavelengths in the range of about 0.4 to 2.0 μm. Some of this electromagnetic energy is absorbed and converted to thermal energy, which heats the atmosphere and surface. The planet cools itself of the absorbed solar radiation in various ways, but ultimately that energy is dissipated by an emission of electromagnetic energy to outer space as longer-wave infrared radiation (of a spectral quality that peaks at a wavelength of 10 μm). In this case, relatively short-wavelength solar radiation is ultimately transformed into the longer-wavelength radiation emitted by Earth, a process that represents a degradation in quality of the energy and an increase in the entropy of the universe.

An important corollary (or secondary proposition) of the second law of thermodynamics is that energy transformations can never be completely efficient—some of the initial content of energy must always be converted to heat so that
entropy increases. This helps to explain why, even when using the best available technology, only about 30% of the potential energy of gasoline can be converted into the kinetic energy of a moving automobile, and no more than about 40% of the energy of coal or natural gas can be transformed into electricity in a generating station. There are also thermodynamic limits to the efficiency of photosynthesis, the process by which plants convert visible radiation into biochemical, even when it is occurring under ideal conditions with optimal supplies of nutrients, water, and light.

A superficial assessment might suggest that life in general appears to contradict the second law of thermodynamics. Plants, for example, absorb visible wavelengths of electromagnetic radiation and use this highly dispersed form of energy to fix simple inorganic molecules (carbon dioxide and water) into extremely complex and energy-dense biochemicals. The plant biomass may then be consumed by animals and microbes, which synthesize their own complex biochemicals. These various bio-syntheses represent energy transformations that greatly decrease local entropy because relatively dispersed electromagnetic energy and simple inorganic compounds are being converted into the complex, highly ordered biochemicals of organisms. Do these biological transformations contravene the second law of thermodynamics?

This seeming paradox of life can be resolved using the following logic: the localized bio-concentration of negative entropy can only occur because the system (ultimately referring to the biosphere, or all life on Earth) receives a constant input of energy in the form of solar radiation. If this external source of energy were somehow terminated, all of the organisms and organic materials would spontaneously degrade, releasing simple inorganic molecules and heat and thereby increasing the entropy of the universe. Therefore, life and ecosystems cannot survive without continual inputs of solar energy, which are required to organize and maintain their negative entropy. In this sense, the biosphere can be viewed as representing an “island” of negative entropy, highly localized in space and time, and continuously fuelled by the Sun as an external source of energy.

Earth: An Energy Flow-Through System

Electromagnetic radiation emitted by the Sun is by far the major input of energy that drives ecosystems. Solar energy heats the planet, circulates its atmosphere and oceans, evaporates its water, and sustains almost all its ecological productivity. Eventually, all of the solar energy absorbed by Earth is re-radiated back to space in the form of electromagnetic radiation of a longer wavelength than what was originally captured. In other words, Earth is a flow-through system, with a perfect balance between the input of solar energy and output of re-radiated energy, and no net storage over the longer term.

In addition, almost all ecosystems absolutely depend on solar radiation as the source of energy that photosynthetic organisms (such as plants and algae) utilize to synthesize simple organic compounds (such as sugars) from inorganic molecules (carbon dioxide and water). Plants and algae then use the chemical potential energy in these sugars, plus inorganic nutrients (such as nitrate and phosphate), to synthesize a huge diversity of biochemicals through various metabolic reactions. Plants grow and reproduce by using these biochemicals and their potential energy. Moreover, plant biomass is used as food by the enormous numbers of organisms that are incapable of photosynthesis. These organisms include herbivores that eat plants directly, carnivores that eat other animals, and detritivores that feed on dead biomass. (The energy relationships within ecosystems are described later.)

Less than 0.02% of the solar energy received at Earth’s surface is absorbed and fixed by photosynthetic plants and
algae. Although this represents a quantitatively trivial component of the planet’s energy budget, it is extremely important qualitatively because this biologically absorbed and fixed energy is the foundation of ecological productivity. Ultimately and eventually, however, the solar energy fixed by plants and algae is released to the environment again as heat and is eventually radiated back to outer space. This reinforces the idea of Earth being a flow-through system for energy, with a perfect balance between the input and output.

Earth’s Energy Budget

An energy budget of a system describes the rates of energy input and output as well as any internal transformations among its various states, including changes in stored quantities. Figure 4.2 illustrates key aspects of the physical energy budget of Earth.

The rate of input of solar radiation to Earth averages about 8.36 J/cm²-minute (2.00 cal/cm²-min), measured at the outer limit of the atmosphere. About half of this energy input is visible radiation and half is near infrared. The output of energy from Earth is also about 8.36 J/cm²-min, occurring as longer-wave infrared. Because the rates of energy input and output are equal, there is no net storage of energy, and the average surface temperature of the planet remains stable. Therefore, as was previously noted, the energy budget of Earth can be characterized as a zero-sum, flow-through system.

However, the above is not exactly true. Over extremely long scales of geological time, a small amount of storage of solar energy has occurred through an accumulation of undecomposed biomass that eventually transformed into fossil fuels. In addition, relatively minor long-term fluctuations in Earth’s surface temperature occur, representing an important element of climate change. Nevertheless, these are quantitatively trivial exceptions to the statement that Earth is a zero-sum, flow-through system for solar energy.

Figure 4.2. Important Components of Earth’s Physical Energy Budget. About 30% of the incoming solar radiation is reflected by atmospheric clouds and particulates and by the surface of the planet. The remaining 70% is absorbed and then dissipated in various ways. Much of the absorbed energy heats the atmosphere and terrestrial surfaces, and most is then re-radiated as long-wave infrared radiation. Atmospheric moisture and greenhouse gases interfere with this process of re-radiation, keeping the surface considerably warmer than it would otherwise be (see also Chapter 17). The numbers refer to the percentage of incoming solar radiation. See the text for a more detailed description of important factors in this energy budget. Source: Modified from Schneider (1989).
Even though the amount of energy emitted by Earth eventually equals the quantity of solar radiation that is absorbed, many ecologically important transformations occur between the initial absorption and eventual re-radiation. These are the internal elements of the physical energy budget of the planet (see Figure 4.2). The most important components are described below:

**Reflection** – On average, Earth’s atmosphere and surface reflect about 30% of incoming solar energy back to outer space. Earth’s reflectivity (albedo) is influenced by such factors as the angle of the incoming solar radiation (which varies during the day and over the year), the amounts of reflective cloud cover and atmospheric particulates (also highly variable), and the character of the surface, especially the types and amounts of water (including snow and ice) and darker vegetation.

**Absorption by the Atmosphere** – About 25% of incident solar radiation is absorbed by gases, vapours, and particulates in the atmosphere, including clouds. The rate of absorption is wavelength-specific, with portions of the infrared range being intensively absorbed by the so-called “greenhouse” gases (especially water vapour and carbon dioxide; see Chapter 17). The absorbed energy is converted to heat and re-radiated as infrared radiation of a longer wavelength than what has been initially absorbed.

**Absorption by the Surface** – On average, about 45% of incoming solar radiation passes through the atmosphere and is absorbed at Earth’s by living and non-living materials at the surface, a transformation that increases their temperature. However, this figure of 45% is highly variable, depending partly on atmospheric conditions, especially cloud cover, and also on whether the incident light has passed through a plant canopy. Although over the longer term (years) and even the medium term (days) the global net storage of heat is essentially zero, in some places there may be substantial changes in the net storage of thermal energy within the year. This occurs everywhere in Canada because of the seasonality of its climate, in that environments are much warmer during the summer than in the winter. Nevertheless, almost all of the absorbed energy is eventually dissipated by re-radiation from the surface as long-wave infrared.

**Evaporation of Water** – Some of the thermal energy of living and non-living surfaces causes water to evaporate in a process known as evapotranspiration. This process has two components: the evaporation of water from lakes, rivers, streams, moist rocks, soil, and other non-living substrates, and transpiration of water from any living surface, particularly from plant foliage, but also from moist body surfaces and lungs of animals.

**Melting of Snow and Ice** – Absorbed thermal energy can also cause ice and snow to melt, representing an energy transformation associated with a change of state of water from a solid to a liquid form.

**Wind and Water Currents** – There is a highly uneven distribution of the content of thermal energy at and near the surface of Earth, with some regions being quite cold (such as the Arctic) and others much warmer warm (the tropics). Because of this irregular allocation of heat, the surface develops processes to diminish the energy gradients by transporting mass around the globe, such as by winds and oceanic currents (see also Chapter 3).

**Biological Fixation** – A very small but ecologically critical portion of incoming solar radiation (globally averaging less than 0.02%) is absorbed by chlorophyll in plants and algae and used to drive photosynthesis. This biological fixation allows some of the solar energy to be temporarily stored as potential energy in biochemicals, thereby serving as the energetic basis for ecological productivity and life on Earth.
Energy in Ecosystems

An ecological energy budget focuses on the absorption of energy by photosynthetic organisms and the transfer of that fixed energy through the trophic levels of ecosystems ("trophic" refers to the means of organic nutrition). Ecologists classify organisms in terms of the sources of energy they utilize.

Autotrophs are capable of synthesizing their complex biochemicals using simple inorganic compounds and an external source of energy to drive the process. The great majority are photoautotrophs, which use sunlight as their external source of energy. Photoautotrophs capture solar radiation using photosynthetic pigments, the most important of which is chlorophyll. Green plants are the most abundant examples of photoautotrophs, but algae and some bacteria are also photoautotrophic.

A much smaller number of autotrophs are chemoautotrophs, which harness some of the energy content of certain inorganic chemicals to drive a process called chemosynthesis. The bacterium Thiobacillus thiooxidans, for example, oxidizes sulphide minerals to sulphate and uses some of the energy liberated during this reaction to chemosynthesize organic molecules.

Because autotrophs are the biological foundation of ecological productivity, ecologists refer to them as primary producers. The total fixation of solar energy by all of the primary producers within an ecosystem is known as gross primary production (GPP). Primary producers use some of this production for their own respiration (R) – that is, for the physiological functions needed to maintain their health and to grow. Respiration is the metabolic oxidation of biochemicals, and it requires a supply of oxygen and releases carbon dioxide and water as waste products. Net primary production (NPP) refers to the fraction of GPP that remains after primary producers have used some for their own respiration. In other words: NPP = GPP – R.

The energy fixed by primary producers is the basis for the productivity of all other organisms, known as heterotrophs, which heterotrophs rely on other organisms, living or dead, to supply the energy they need. Animal heterotrophs that feed on plants are known as herbivores (or primary consumers); three familiar examples are deer, geese, and grasshoppers. Heterotrophs that consume other animals are known as carnivores (or secondary consumers), such as timber wolf, peregrine falcon, sharks, and spiders. Some species feed on both plant and animal biomass and are known as omnivores – the grizzly bear is a good example, as is our own species. Many other heterotrophs feed primarily on dead organic matter and are called decomposers or detritivores, such as vultures, earthworms, and most fungi and bacteria.

Image 4.3. Plant productivity is sustained by solar energy, which is fixed by chlorophyll in the plant and used to combine carbon dioxide, water, and other simple inorganic compounds into the complex molecular structures of organic matter. These ecologists are studying the productivity of a plant community on Sable Island, Nova Scotia. Source: B. Freedman.
Productivity is production expressed as a rate function, that is, per unit of time and area. Productivity in terrestrial ecosystems is often expressed in units such as kilograms of dry biomass (or its energy equivalent) per hectare per year (kg/ha-y or kJ/ha-y), while aquatic productivity is often given as grams per cubic metre per year (g/m\(^3\)-y).

Many studies have been made of the productivity of the various trophic levels in ecosystems. For example, studies of a natural oak–pine forest found that the total fixation of solar energy by the vegetation (the annual gross primary production) was equivalent to 4.81 \(\times\) 104 kJ/m\(^2\)-y (48 100 kJ/m\(^2\)-y) (Odum, 1993). This fixation rate was equivalent to less than 0.1% of the annual input of solar radiation. Because the plants used 2.72 \(\times\) 104 kJ/m\(^2\)-y during their respiration, the net primary productivity was 2.09 \(\times\) 104 kJ/m\(^2\)-y, represented mainly by the growing biomass of the trees. The various heterotrophic organisms in the forest used 1.26 \(\times\) 104 kJ/m\(^2\)-y to support their respiration. Ultimately, the net accumulation of biomass by all organisms in the ecosystem (referred to as the net ecosystem productivity) was equivalent to 0.83 \(\times\) 104 kJ/m\(^2\)-y, or 8.3 \(\times\) 103 kJ/m\(^2\)-y.

The primary productivities of the world’s major classes of ecosystems are summarized in Table 4.1. Note that the rate of production is greatest in tropical forests, wetlands, coral reefs, and estuaries. The production for each ecosystem type is calculated as its productivity multiplied by its area. However, the largest amounts of production occur in tropical forests and the open ocean. Note that the open ocean has a relatively small productivity, but its global production is large because of its enormous area.

Table 4.1. Primary Production of Earth’s Major Ecosystems. The ecosystems are listed in order of net primary productivity. Productivity is the rate of production, standardized to area and time, while production is the total amount of biomass (in dry tonnes) produced by the global area of an ecosystem. See Chapter 8 for descriptions of these biomes (major kinds of ecosystems). Source: modified from Whittaker and Likens (1975).
<table>
<thead>
<tr>
<th>Biome (ecosystem)</th>
<th>Area ($10^6$ km$^2$)</th>
<th>Net Primary Productivity ($10^6$ T/yr)</th>
<th>Global Net Production ($10^9$ T/yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wetlands</td>
<td>2</td>
<td>30</td>
<td>6</td>
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<tr>
<td>Tropical rain forest</td>
<td>17</td>
<td>22</td>
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<tr>
<td>Tundra, arctic and alpine</td>
<td>2</td>
<td>4</td>
<td>0.8</td>
</tr>
<tr>
<td>Desert &amp; semi-desert shrubland</td>
<td>18</td>
<td>0.9</td>
<td>1.6</td>
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<td>Extreme desert</td>
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<td>Reefs &amp; estuaries</td>
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