Energy in the Ecosystem

Alfred J. Lotka developed the first thermodynamic concept of the ecosystem.

Primary production is the assimilation of energy and production of organic matter by photosynthesis.

Only 5% to 20% of energy passes between trophic levels.

Energy moves through ecosystems at different rates.

Ecosystem energetics summarizes the movement of energy through the ecosystem.

We humans consume a large proportion of the earth's production. The total production of dry plant biomass over the surface of the earth amounts to 224 billion tons per year. Of this, approximately 59% is produced in terrestrial ecosystems. Of that terrestrial production, an astonishing 35% to 40% is used by humans, either directly as food and fiber crops or indirectly as feed for animals.

The oceans, traditionally a source of food for people living near the coast, are now becoming a major source of food for much of the world's population. By the early 1980s, the global fish catch amounted to 75 million tons per year, and this has since increased substantially.

How much of the production of algae in the oceans is required to sustain the fisheries on which humans depend? How much of the total algal production is represented in the 75 million tons of fish and other seafood we harvest each year? How much more food can we expect to harvest from the oceans? Two marine ecologists, D. Pauly and V. Christensen, who were working at the International Center for Living Aquatic Resources Management in the Philippines, sought to answer these questions from their understanding of energy flow in natural ecosystems.

Pauly and Christensen assumed that for each step in the chain of feeding relationships that leads from microscopic algae to the fish we eat, about 90% of consumed energy is used to maintain the consumer. This means that only 10% is converted through growth and reproduction to biomass, and thus potential food for other organisms. From studies of the diets of marine organisms, Pauly and Christensen estimated the number of feeding steps leading from algae to fish. These varied from averages of about 1.5 for coastal and reef ecosystems to 3 for the open ocean. Knowing the number of feeding steps and assuming an energy transfer efficiency of 10% per step, they used a simple calculation to convert harvested fish into amounts of algae.
needed to sustain them. Such calculations showed that for inshore fisheries, which produce most of the fish consumed by humans, the algal growth required to sustain the harvested fish amounted to 24% to 35% of the total production of the ecosystem. Because much of the production in these systems consists of species not eaten by humans, our harvesting may be approaching its upper limit. Only in the open ocean, which is much more difficult for humans to exploit, do we usurp a small fraction (about 2%) of the total production.

During the early part of the twentieth century, several new concepts emerged that led the study of ecology in novel directions. One of these was the realization that feeding relationships link organisms into a single functional entity. Foremost among the proponents of this new ecological viewpoint during the 1920s was the English ecologist Charles Elton. Elton argued that organisms living in the same place not only had similar tolerances of physical factors in the environment, but also interacted with one another, most importantly in a system of feeding relationships that he called a food web. Of course, every organism must feed in some manner to gain nourishment, and each may be fed upon by some other organism. However, regarding these feeding relationships as an ecological unit was a novel idea early in the twentieth century.

A decade later, the English plant ecologist A. G. Tansley took Elton’s idea an important step further by considering animals and plants, together with the physical factors of their surroundings, as ecological systems. Tansley called this concept the ecosystem, and regarded it as the fundamental unit of ecological organization. Tansley envisioned the biological and physical parts of nature together, unified by the dependence of animals and plants on their physical surroundings and by their contributions to maintaining the conditions and composition of the physical world.

Alfred J. Lotka developed the first thermodynamic concept of the ecosystem

Working independently of the ecologists of his day, Alfred J. Lotka, a chemist by training, was the first to consider populations and communities as energy-transforming systems. He suggested that each system can be described in principle by a set of equations that represent exchanges of matter and energy among its components. Such exchanges include the assimilation of carbon dioxide into organic carbon compounds by plants, the consumption of plants by herbivores, and the consumption of animals by carnivores.

Lotka believed that the size of a system and the rates of energy and material transformations within it obeyed certain thermodynamic principles that govern all energy transformations. Just as heavy machines and fast machines require more fuel to operate than lighter and slower ones, and inefficient machines require more fuel than efficient ones, the energy transformations of ecosystems grow in direct proportion to their size (roughly, the total mass of their constituent organisms), productivity (rate of transformations), and inefficiency. The earth itself is a giant thermodynamic machine in which the circulation of winds and ocean currents and the evaporation of water are driven by the energy in sunlight. Part of that energy is assimilated by the photosynthesis of plants, and this energy ultimately fuels all biological systems.

Lotka’s ideas were not widely appreciated by ecologists of his time. His mathematical representations were difficult and unfamiliar, and he did little to promote his ideas. The concept of the ecosystem as an energy-transforming system was brought to the attention of many ecologists for the first time in 1942 by Raymond Lindeman, a young aquatic ecologist at the University of Minnesota. Lindeman’s framework for understanding ecological systems on the basis of thermodynamic principles made a deep impression. He adopted Tansley’s notion of the ecosystem as the fundamental unit in ecology and Elton’s concept of the food web, including inorganic nutrients at the base, as the most useful expressions of ecosystem structure.

The sequence of feeding relationships by which energy passes through the ecosystem is referred to as a food chain. A food chain has many links—plant, herbivore, and carnivore, for example—which Lindeman referred to as trophic levels. (The Greek root of the word trophic means “food.”) Furthermore, Lindeman visualized a pyramid of energy within the ecosystem, with less energy reaching each successively higher trophic level (Figure 6.1). Lindeman argued that energy is lost at each level because of the work performed by organisms at that level and because of the inefficiency of biological energy transformations. Thus, plants gather only a portion of the light energy available from the sun. Herbivores harvest even less of that light energy because plants use a portion of the energy they assimilate to maintain themselves, and that energy is not available to herbivores as plant biomass. The same may be said of the consumers of herbivores, and of each successively higher level of the food chain.

By the 1950s, the ecosystem concept had fully pervaded ecological thinking and had spawned a new branch of ecology, called ecosystem ecology, in which
the cycling of matter and the associated passage of energy through an ecosystem provided a basis for characterizing that system's structure and function. Energy and the masses of elements, such as carbon, provided a common "currency" that ecologists could use to compare the structure and functioning of different ecosystems in terms of the energy and matter residing in, and transferred among, the plants, animals, microbes, and abiotic components of the ecosystem. Measurements of energy assimilation and energetic efficiencies became the tools for exploring this new thermodynamic concept of the ecosystem.

With this new conceptual framework, ecologists began to measure energy flow and the cycling of nutrients. One of the strongest proponents of this approach has been Eugene P. Odum of the University of Georgia, whose text *Fundamentals of Ecology*, first published in 1953, influenced a generation of ecologists. Odum depicted ecosystems as energy flow diagrams (Figure 6.2a). For any one trophic level, such a diagram features a box representing the biomass (or its energy equivalent) of all the organisms making up that trophic level at any given time. For example, a box might represent all the plants or all the herbivores in a particular ecosystem. Superimposed on this box are pathways representing the flow of energy through that trophic level. These diagrams simplified nature, but nonetheless conveyed the important principle that energy passes from one

![Figure 6.1](image) An ecological pyramid of energy. The breadth of each bar represents the net productivity of a trophic level in the ecosystem. For this particular system, ecological efficiencies are 20%, 15%, and 10% between trophic levels, but these values vary widely in different communities.

![Figure 6.2](image) E. P. Odum's "universal" model of ecological energy flow. (a) A single trophic level. (b) Representation of a food chain. The net production of one trophic level becomes the ingested energy of the next higher level.
link in the food chain to the next, diminished by respiration and the shunting of unused foodstuffs to detritus-based food chains. Odum depicted feeding relationships as two or more energy flow diagrams linked into food chains, as shown in Figure 6.2b.

Unlike energy, which enters ecosystems as light and leaves as heat, nutrients are regenerated and retained within the system. Odum extended his model to include this cycling of elements. He showed that matter cycles within the ecosystem, being taken up in inorganic forms by plants and converted to biomass and eventually returned to inorganic forms by the process of decomposition. The most obvious recycling of material in this manner is the production of carbon dioxide by respiration and its uptake by plants during photosynthesis. However, each element is eventually returned to an inorganic form in its cycle through the ecosystem. In ecosystem energetics, studies of the cycling of elements have assumed equal standing with studies of the flow of energy. Amounts of elements and their movement among ecosystem components provide a convenient index to the flow of energy, which is difficult to measure directly. For instance, because light energy is transferred to the chemical energy content of organic molecules during photosynthesis, tracking of the movement of biological forms of carbon can be used to follow the movement of energy through the ecosystem.

A second reason for the prominence of nutrient cycling in ecosystem ecology is the fact that, in many circumstances, the quantities of certain nutrients regulate the production of biomass by plants, which is the material and energetic base of the entire ecosystem. For example, availability of water, rather than sunlight or minerals in the soil, limits the productivity of desert plants. In contrast, the open oceans are deserts by virtue of their scarce nutrients, particularly nitrogen. Understanding how elements cycle among components of the ecosystem is crucial to understanding the regulation of ecosystem structure and function.

### Primary production: the assimilation of energy and production of organic matter by photosynthesis

Plants, algae, and some bacteria capture light energy and transform it into the energy of chemical bonds in carbohydrates. This process is referred to as primary production, and its rate is quantified as primary productivity. As we have seen, photosynthesis chemically unites two common inorganic compounds, carbon dioxide (\( \text{CO}_2 \)) and water (\( \text{H}_2\text{O} \)), to form the sugar glucose (\( \text{C}_6\text{H}_{12}\text{O}_6 \)), with the release of oxygen (\( \text{O}_2 \)). The overall chemical balance of the photosynthetic reaction is

\[
6\text{CO}_2 + 6\text{H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2.
\]

Photosynthesis transforms carbon from an oxidized (low-energy) state in \( \text{CO}_2 \) to a reduced (high-energy) state in carbohydrates. Because work is performed on the carbon atoms to increase their energy level, photosynthesis requires energy. This energy is provided by visible light. In quantitative terms, for each gram of carbon assimilated, a plant transfers 39 kilojoules (kJ) of energy from sunlight to the chemical energy of carbon in carbohydrates.

The pigments that capture the energy of light for photosynthesis actually absorb only a small fraction of the total incident solar radiation. In addition, because of inefficiencies in the many biochemical steps of photosynthesis, plants assimilate no more than a third (and usually much less) of the light energy absorbed by those photosynthetic pigments. The rest is lost as heat.

Photosynthesis supplies the carbohydrates and energy that a plant needs to build tissues and grow. Rearranged and joined together, glucose molecules become fats, starches, oils, and cellulose. Glucose and other organic compounds (starches and oils, for example) may be transported throughout the plant or stored as a source of energy for future needs. Combined with nitrogen, phosphorus, sulfur, and magnesium, simple carbohydrates derived from glucose produce an array of proteins, nucleic acids, and pigments. Plants cannot grow unless they have all these basic building materials. For example, the photosynthetic pigment chlorophyll contains an atom of magnesium, and so even when all other necessary elements are present in abundance, a plant lacking sufficient magnesium cannot produce chlorophyll, and thus cannot engage in photosynthesis.

Plants and other photosynthetic autotrophs form the base of all food chains, and therefore they are referred to as the primary producers of the ecosystem. Ecologists are interested in the rate of primary production because this determines the total energy available to the ecosystem. The total energy assimilated by photosynthesis is referred to as gross primary production. Plants use some of this energy to support the synthesis of biological compounds and to maintain themselves, and so their biomass contains substantially less energy than the total assimilated (Figure 6.9). The energy accumulated in plants, and which is therefore available to consumers, is referred to as net primary production. The difference between gross and net primary production is the energy of respiration, which is the amount used by plants for maintenance and biosynthesis.
**ECOLOGISTS IN THE FIELD**

Primary production can be measured by gas exchange or the growth of plants.

Plant production involves fluxes of carbon dioxide, oxygen, minerals, and water and the accumulation of biomass (Figure 6.4). In principle, the rates of any of these flows could provide an index to the rate of primary production. It is worth discussing the measurement of primary production in some detail, as this will provide a better understanding of the processes involved in production and of the difference between gross and net production.

The unit of production is energy per unit of area per unit of time. For comparing production, ecologists often use kilojoules per square meter per year (kJ per m² per yr) or watts per square meter (W per m²). Production need not be measured only in terms of energy, however. Net production can be quantified conveniently as grams of carbon assimilated, dry weight of plant tissues, or their energy equivalents. Ecologists use such indices interchangeably because they are highly correlated. The energy equivalent of an organic compound depends primarily on its carbon content. Organic compounds contain approximately 39 kJ of metabolizable energy per gram of carbon, with some energy added or subtracted during various biochemical transformations.

In terrestrial ecosystems, ecologists often estimate net production by the amount of plant biomass produced in a year. In areas of seasonal growth, annual production may be estimated by cutting, drying, and weighing plants at the end of the growing season. Clearly, such harvesting methods measure net, rather than gross, production. Root growth is often ignored because roots are difficult to remove from most soils; thus harvesting measures annual aboveground net productivity (ANP), the most common basis for comparing terrestrial communities. Production of small plants or individual leaves is most often quantified directly by carbon dioxide uptake. Because the atmosphere contains so little carbon dioxide (0.03%), plants can measurably reduce its concentration in an enclosed chamber within a short period. This change in CO₂ concentration can provide a direct estimate of photosynthetic rate. A convenient application of this method is to enclose leaves (or whole herbaceous plants or branches of trees) in a clear chamber (light must penetrate for photosynthesis) and measure the change in the concentration of CO₂ in air passed through the chamber. The technology for doing this is now so advanced that rates of carbon dioxide uptake can be measured on a few square centimeters of leaf under natural conditions in a matter of seconds. The change in CO₂ concentration per gram of dry weight or per square centimeter of leaf surface area is then extrapolated to the

**Figure 6.4** The fluxes involved in photosynthesis can be measured and used to estimate primary productivity.
entire tree or forest. When a plant is exposed to light, carbon dioxide flux includes both assimilation (uptake) and respiration (output), and thus measures net production. Respiration can be measured separately by carbon dioxide production in the absence of light. Gross production can then be estimated by adding respiration to the net production (Figure 6.5).

The radioactive isotope carbon-14 (\(^{14}\text{C}\)) provides a useful variation on this method of measuring productivity. When a known amount of \(^{14}\text{C}\)-labeled carbon dioxide is added to an airtight chamber, plants assimilate the radioactive carbon atoms roughly in proportion to their occurrence in the air inside the chamber. Thus, the rate of carbon fixation can be calculated by dividing the amount of \(^{14}\text{C}\) in the plants by the proportion of \(^{14}\text{C}\) in the chamber at the beginning of the experiment. For example, if a plant takes up 10 mg of \(^{14}\text{C}\) in an hour, and \(^{14}\text{C}\) constitutes 5% of the carbon in the chamber, we can conclude that the plant assimilates carbon at a rate of about 200 mg per h (10 divided by 0.05).

In aquatic systems, harvesting provides a convenient method for estimating the primary production of large photosynthetic organisms, such as kelps, but this technique is not practical for small organisms, such as phytoplankton. Because of the high concentrations of bicarbonate in most waters, measuring changes in carbon dioxide in aquatic systems is not practical either. However, because oxygen dissolves so poorly in water, one can measure small changes in oxygen concentration in most aquatic systems. Remember that photosynthesis produces molecular oxygen (\(\text{O}_2\)) as a by-product. To estimate primary production, samples of water containing phytoplankton are suspended in pairs of sealed bottles at desired depths beneath the surface of a body of water. One bottle (the 'light bottle') is clear and allows sunlight to enter; the other (the 'dark bottle') is opaque (Figure 6.6). In the light bottle, photosynthesis and respiration occur together, and part of the oxygen produced by the first process is consumed by the second. In the dark bottle, respiration consumes oxygen without it being replenished by photosynthesis. Thus, gross production can be estimated by adding the change in oxygen concentration in the dark bottle (respiration alone) to that in the light bottle (photosynthesis and respiration). In unproductive waters, such as those of deep lakes and the open ocean, changes in oxygen concentration are too slow to measure easily. In such situations, the uptake of \(^{14}\text{C}\) by plants and algae provides a more sensitive measure of carbon assimilation.

**Light and temperature influence rates of photosynthesis**

Primary production is sensitive to variations in light and temperature. For plants growing in full sunlight, light levels usually exceed the saturation point of their photosynthetic pigments (see Figure 3.10); therefore the photosynthetic rate of such plants generally is not restricted by light availability. For plants growing in shade or at depth in aquatic systems, however, the rate of photosynthesis often is limited by light. In addition, any particular leaf does not al-
ways operate at its maximum possible photosynthetic rate. Cloud cover, shading by other leaves or plants, and low levels of light early and late in the day reduce the photosynthetic rate below its maximum.

Photosynthetic efficiency is the percentage of the energy in sunlight that is converted to net primary production during the growing season. This measure provides a useful index to rates of primary production under natural conditions. Where water and nutrients do not limit plant production severely, the photosynthetic efficiency of an ecosystem as a whole varies between 1% and 2%. What happens to the remaining 98–99% of the light energy? Leaves and other surfaces reflect anywhere from 25% to 75% of it. Molecules other than photosynthetic pigments absorb most of the remainder, which is converted to heat and either radiated or conducted across the leaf surface or dissipated by the evaporation of water from the leaf (transpiration).

Like the rates of most other physiological processes, the rate of photosynthesis generally increases with temperature, at least up to a point. The optimum temperature for photosynthesis varies with the prevailing temperature of the environment—from about 16°C in many temperate species to as high as 38°C in tropical species. Net production depends on the rate of respiration as well as on the rate of photosynthesis, and respiration generally increases with increasing leaf temperature as well. Thus, net production, and therefore net assimilation of CO₂, may actually decrease with increased temperature.

Water limits primary production in many terrestrial habitats

As we saw in Chapter 3, the tiny openings (stomata) in leaves through which carbon dioxide and oxygen are exchanged with the atmosphere also allow water to leave the leaf by transpiration. When the soil moisture approaches a plant’s wilting point, the stomates close to reduce water loss. This prevents uptake of CO₂, and photosynthesis slows to a standstill. Consequently, the rate of photosynthesis depends on the availability of soil moisture, a plant’s ability to tolerate water loss, and the influence of air temperature and solar radiation on the rate of transpiration.

Agronomists quantify the drought resistance of crop plants in terms of transpiration efficiency, also called water use efficiency, which is the number of grams of dry matter produced (net production) per kilogram of water transpired. In most plants, transpiration efficiencies are less than 2 g of production per kilogram of water, but they may be as high as 4 g per kilogram in drought-tolerant crops. Because transpiration efficiency varies little among a wide variety of plant species, production can be directly related to water availability in the environment, as we saw in the case of maize crops in Zimbabwe (see Figure 4.16). However, much of the precipitation received by an area is never taken up by plants. Ground water, surface water (streams), and evaporation from the soil account for the remainder of the water budget. For example, in perennial grassland in southern Arizona, production varies in direct proportion to precipitation during the summer growing season, but at a rate of only about 200 kilograms of dry matter per hectare for each 10 cm of precipitation. Ten centimeters of rainfall is equivalent to 1 million kilograms of water per hectare. Thus, the water use efficiency of the grassland biome as a whole is only 0.2 g per kilogram, about one-tenth that based on transpired water. This finding indicates that only about 10% of the precipitation is taken up and transpired by plants in this habitat. Most of the rain comes in extremely heavy thundershowers during the summer months, and most of the water quickly runs off the land.

Nutrients stimulate plant production in both terrestrial and aquatic ecosystems

Fertilizers stimulate plant growth in most environments. When nitrogen and phosphorus fertilizers were applied singly and in combination to chaparral habitat in southern California, most species responded with increased production to additions of nitrogen, but not phosphorus (Figure 6.7). This result suggests that production in most chaparral species is limited by the availability of nitrogen. However, the growth of California lilac bushes (Ceanothus greggi), which harbor nitrogen-fixing bacteria in their root systems, responded to the addition of phosphorus, but not to nitrogen. The production of annual plants (forbs and grasses) in the same environment increased when nitrogen was applied, but was depressed somewhat by the application of phosphorus alone. When equal amounts of nitrogen and phosphorus were applied together, however, production soared. Evidently, the annual plants could take advantage of increased phosphorus only in the presence of high levels of nitrogen.

Nutrients limit primary production most strongly in aquatic environments, particularly in the open ocean, where the scarcity of dissolved minerals reduces production far below terrestrial levels. Even in shallow coastal waters, where vertical mixing, upwelling currents, and runoff from the land maintain nutrients at high concentrations, the addition of fertilizers (as often occurs inadvertently through pollution) may greatly enhance aquatic production, upsetting the natural balance of aquatic ecosystems.
Primary production varies among ecosystems

The favorable combination of intense sunlight, warm temperature, abundant rainfall, and ample nutrients in parts of the humid Tropics results in the highest terrestrial productivity on earth. In temperate and arctic ecosystems, low winter temperatures and long winter nights curtail production. Within a particular latitude belt, where light does not vary appreciably from one locality to the next, net production is related directly to temperature and annual precipitation. Above a certain threshold of water availability, net production increases by 0.4 g of dry matter per kilogram of water in hot deserts and by 1.1 g per kilogram in short-grass prairies and cold deserts. Thus, a given amount of water supports almost three times as much plant production in the cooler climates as in the hotter climates within a given latitudinal belt.

Global patterns of net primary production are summarized in Figure 6.8. The production of terrestrial vegetation is highest in the humid Tropics and lowest in tundra and desert habitats. Swamp and marsh ecosystems, which occupy the interface between terrestrial and aquatic habitats, can produce as much biomass annually as tropical forests because of the continuous availability of water and the rapid regeneration of nutrients in mucky sediments surrounding plant roots.

In the open ocean, scarcity of mineral nutrients limits productivity to a tenth that of temperate forests, or even less. Upwelling zones where nutrients reach the surface from deeper waters and continental shelf areas where bottom sediments in shallow water rapidly exchange nutrients with surface waters support greater production. In estuaries, coral reefs, and coastal algal beds, production approaches levels observed in terrestrial habitats. Primary production in freshwater environments is considerably higher than that in the open oceans, achieving the highest levels in rivers, shallow lakes, and ponds and the lowest levels in clear streams and deep lakes.

Only 5% to 20% of energy passes between trophic levels

Primary production by plants, algae, and some bacteria forms the base of ecological food chains. Animals, fungi, and most microorganisms obtain their energy and most of their nutrients from plants or animals, or the dead remains of either. These organisms, therefore, have dual roles as food producers and food consumers. These roles give the ecosystem a trophic structure that is determined by food webs through which energy flows and nutrients cycle. The
Ecologists refer to the percentage of energy transferred from one trophic level to the next as ecological efficiency or food chain efficiency. To understand why ecological efficiencies are only 5–20%, we must examine how organisms make use of the energy they consume.

Regardless of the source of its food, an organism uses the energy from that food to maintain itself, to fuel its activities, and to grow and reproduce. Once ingested, the energy in food follows a variety of paths through the organism. To begin with, many components of food are not easily digested: hair, feathers, insect exoskeletons, cartilage, and bone in animal foods, and cellulose and lignin in plant foods (Figure 6.9). These substances may be defecated or regurgitated, and the energy they contain is referred to as egested energy. What an organism digests and absorbs constitutes its assimilated energy. The portion of this assimilated energy used to meet metabolic needs, most of which escapes the organism as heat, makes up the respired energy. Animals excrete another, usually smaller, portion of the assimilated energy in the form of nitrogen-containing organic wastes (primarily ammonia, urea, or uric acid), produced when the diet contains an excess of nitrogen; this is called excreted energy. Assimilated energy
Assimilation efficiency depends on the digestibility of the diet

The overall ecological efficiency of the food chain begins with the efficiency with which organisms assimilate the food they consume. **Assimilation efficiency** is the ratio of assimilation to ingestion, usually expressed as a percentage. The energy value of plants to their consumers depends on their food quality—that is, on how much cellulose, lignin, and other indigestible materials they contain. Herbivores assimilate as much as 80% of the energy in seeds and 60–70% of that in young vegetation. Most grazers and browsers (elephants, cattle, grasshoppers) extract 30–40% of the energy in their food. Millipedes, which eat decaying wood composed mostly of cellulose and lignin (and the microorganisms that occur in decaying wood), assimilate only 15% of the energy in their diet.

Food of animal origin is more easily digested than food of plant origin. Assimilation efficiencies of predatory species range from 60% to 90%. Vertebrate prey are digested more efficiently than insect prey because the indigestible exoskeletons of insects constitute a larger proportion of the body than the hair, feathers, and scales of vertebrates. Assimilation efficiencies of insect eaters vary between 70% and 80%.

**The most active animals have the lowest net production efficiencies**

Each organism grows and produces offspring. The biomass it adds in this manner represents the organism’s production, and is also potentially food for other organisms. The ratio of the energy contained in this production to the total assimilated energy is referred to as **net production efficiency**, and is usually expressed as a percentage. Active, warm-blooded animals exhibit low net production efficiencies: those of birds are less than 1% and those of small mammals with high reproductive rates range up to 6% (Figure 6.10). These organisms use most of their assimilated energy to maintain salt balance, circulate blood, produce heat for thermoregulation, and move. In contrast, sedentary, cold-blooded animals, particularly aquatic species, channel as much as 75% of their assimilated energy into growth and reproduction.

Production efficiency can be based on total energy ingested rather than on energy assimilated. In this case, it is referred to as **gross production efficiency**, which is the product of assimilation efficiency and net production efficiency. Thus,

\[
gross \text{ production efficiency} = \frac{(\text{assimilation/ingestion})}{\times (\text{production/assimilation})} \times 100 = \frac{(\text{production/ingestion})}{\times 100}.
\]
Cross production efficiency represents the overall energetic efficiency of biomass production within a trophic level. Gross production efficiencies of warm-blooded terrestrial animals rarely exceed 5%, and those of some birds and large mammals fall below 1%. For insects, these efficiencies lie within the range of 5% to 15%, and for some aquatic animals they exceed 30%.

Production efficiency in plants
The concept of production efficiency differs somewhat between plants and animals because plants do not digest and assimilate food. For plants, net production efficiency is defined as the ratio of net production to gross production. Net production efficiency varies between 30% and 85% in plants, depending on environment and growth form. Rapidly growing plants in temperate zones—whether trees, old-field herbs, crop species, or aquatic plants—have uniformly high net production efficiencies, typically between 75% and 85%. Similar types of vegetation in the Tropics exhibit lower net production efficiencies (40–60%). As we might expect because of the higher temperature, respiration increases relative to photosynthesis in tropical latitudes.

Detritus food chains
Terrestrial plants, especially woody species, allocate much of their production to structures that are difficult to ingest, let alone digest. As a result, even though herbivores have specialized adaptations to extract energy from plants, they still tend to have low assimilation efficiencies. Consequently, most of the production of terrestrial plants is consumed as detritus—dead remains of plants and undigestible excreta of herbivores—by organisms specialized to attack wood, leaf litter, and fibrous plant egglings. This partitioning between herbivory and detritus feeding establishes two parallel food chains in terrestrial communities (Figure 6.11). The first originates when relatively large animals feed on leafy vegetation, fruit, and seeds; the second originates when relatively small animals and microorganisms consume detritus in the litter and soil. These separate food chains sometimes mingle considerably at higher trophic levels, but the energy of detritus tends to move into the food chain much more slowly than the energy assimilated by herbivores.

The relative importance of herbivore-based and detritivore-based food chains varies greatly among communities. Herbivores predominate in plankton communities,
detritivores in terrestrial communities. The proportion of net production that enters each of these food chains depends on the relative allocation of plant tissue between structural and supportive functions, on one hand, and growth and photosynthetic functions, on the other. A variety of studies have shown that herbivores consume 1.5–2.5% of the net primary production in temperate deciduous forests, 12% of that in old-field habitats, and 60–99% of that in plankton communities.

**Exploitation efficiency**

Because most biological production is consumed by one organism or another, little energy accumulates in any one trophic level. Rather, a balance is achieved between the production of biomass at one level and its consumption at another, so that the trophic structure of an ecosystem remains relatively constant. Viewed in this way, the ecological efficiency of a particular link in the food chain is equivalent to gross production efficiency. Under some conditions, however, production and consumption are not balanced, and energy may accumulate in an ecosystem, whether as organic matter in soil or as organic sediments in aquatic ecosystems. In such a case, we may say that exploitation efficiency—that is, the proportion of production on one trophic level that is consumed by organisms on the next higher level—is less than 100%. In this case, the overall ecological efficiency of the ecosystem is discounted by the exploitation efficiency:

\[
\text{ecological efficiency} = \text{exploitation efficiency} \times \text{gross production efficiency}.
\]

**Energy moves through ecosystems at different rates**

Ecological efficiencies describe what proportion of the energy assimilated by plants eventually reaches each higher trophic level of an ecosystem. The rate of transfer of energy between trophic levels or, inversely, its *residence time* in each trophic level, provides a second index to the energy dynamics of an ecosystem. For a given rate of production, the residence time of energy and the storage of energy in living biomass and detritus are directly related: the longer the residence time, the greater the accumulation of energy (Figure 6.12).

![Figure 6.12: Copepods and other zooplankton cycle the energy and nutrients in their algal food very rapidly. Photo (a) by M. I. Walker/Science Source/Photo Researchers; photo (b) by Roland Birke/Photo Researchers.](image-url)
The average residence time of energy at a particular trophic level equals the energy stored divided by the rate at which energy is converted into biomass:

\[
\text{residence time (yr)} = \frac{\text{energy stored in biomass (kJ per m}^2\text{)}}{\text{net productivity (kJ per m}^2\text{ per yr)}}
\]

We may also calculate the residence time defined by this equation in terms of mass rather than energy, in which case it expresses the \textit{biomass accumulation ratio}. Accordingly,

\[
\text{biomass accumulation ratio (yr)} = \frac{\text{biomass (kg per m}^2\text{)}}{\text{rate of biomass production (kg per m}^2\text{ per yr)}}
\]

Plants in humid tropical forests produce dry matter at an average rate of 1.8 kg per m\(^2\) per yr and have an average living biomass of 42 kg per m\(^2\). Inserting these values into the above equation, we obtain 23 years (42/1.8) for the average residence time of biomass in plants. Biomass accumulation ratios for primary producers may average from more than 20 years in forested terrestrial environments to less than 20 days in aquatic phytoplankton-based communities (\textbf{Figure 6.13}). In all ecosystems, however, some energy remains for a long time, and some disappears quickly. For example, leaf eaters and root feeders consume much of the energy assimilated by forest trees during the year of its production, some of it within days of assimilation by the plant. Energy accumulated in the cellulose and lignin in the trunks of trees, on the other hand, may not be recycled for centuries.

Figure 6.13 underestimates the average residence time of energy in energy-containing organic matter because it does not include the accumulation of dead organic matter in leaf litter. The residence time of energy in accumulated litter can be determined by an equation analogous to that for the biomass accumulation ratio:

\[
\text{residence time (yr)} = \frac{\text{litter accumulation (g per m}^2\text{)}}{\text{rate of litter fall (g per m}^2\text{ per yr)}}
\]

For forested ecosystems, this value varies from 3 months in the humid Tropics to 1–2 years in dry and montane tropical habitats, 4–16 years in the southeastern United States, and more than 100 years in temperate mountains and boreal regions. Warm temperatures and the abundance of moisture in lowland tropical regions create optimal conditions for rapid decomposition of litter.
Ecosystem energetics summarizes the movement of energy through the ecosystem

The flux of energy and the efficiency of its transfer describe certain aspects of the structure of an ecosystem: number of trophic levels, relative importance of detritus feeding and herbivory, steady-state values for biomass and accumulated detritus, and turnover rates of organic matter. The importance of these measures to understanding ecosystem function was argued by Lindeman, who constructed the first energy budget for an entire biological community—that of Cedar Bog Lake in Minnesota (Figure 6.14). The proliferation of energy flow studies during the 1950s and 1960s clearly reflected energy’s acceptance as a universal currency, a common denominator to which all populations and their acts of consumption could be reduced.

The overall energy budget of an ecosystem reflects a balance between income and expenditure, just as in a bank account. The ecosystem gains energy through the photosynthetic assimilation of light by autotrophs and through the transport of organic matter into the system from external sources. Organic materials produced outside the system are referred to as allochthonous inputs (from the Greek chthonos, “of the earth,” and allo, “other”; Figure 6.15). Photosynthesis that occurs within the system is referred to as autochthonous production. In Root Spring, near Concord, Massachusetts, the herbivores assimilated energy at a rate of 0.31 W per m², but the net productivity of aquatic plants and algae was only 0.09 W per m²; the balance was transported into the spring in the form of leaves from nearby vegetation. In general, autochthonous production predominates in large rivers, lakes, and most marine ecosystems; allochthonous imports make up the largest part of energy flux in small streams and springs under the closed canopies of forests. Life in caves and the abyssal depths of the oceans, to which no light penetrates, subsists entirely on energy transported in from outside.

Lindeman constructed the Cedar Bog Lake energy budget from measurements of the harvestable net production at each of three trophic levels—plants and algae, herbivores, and carnivores—and from laboratory determinations of respiration and assimilation efficiencies. Lindeman’s findings were somewhat starting in that the herbivores consumed only 20% of net primary production, and the carnivores consumed only 33% of the net production of the herbivores. These are extremely low exploitation efficiencies. The majority of plant and herbivore biomass that was not consumed ended up as organic sediments at the bottom of the lake.

Even with this sedimentation, the Cedar Bog Lake ecosystem achieved a 12% overall ecological efficiency of energy transfer between trophic levels. After comparing similar analyses of other aquatic communities, ecologist D. G. Kozlovski concluded that (1) assimilation efficiency increases at higher trophic levels; (2) net and gross production efficiencies decrease at higher trophic levels; and (3) ecological efficiency averages about 10%. A simple, and rather surprising, consequence of this 10% rule of thumb for ecological efficiencies is that only 1% of the total energy assimilated by plants and algae ends up as production on the third trophic level. Very little energy is available to support consumers at even higher trophic levels. Thus, as shown in Figure 6.1, the pyramid of energy narrows very quickly as one climbs from one trophic level to the next. For humans, who already command a large proportion of the total primary production of the earth for their own use, this means that food supplies can be increased primarily by eating lower on the food chain—that is, eating more plant products and fewer animal products.

Summary

1. An ecosystem is the entire complex of organisms and the physical environments they inhabit. It is also a giant thermodynamic machine that dissipates energy continu-
ously in the form of heat. This energy initially enters the biological realm of the ecosystem via photosynthesis and plant production, which provide energy for animals and nonphotosynthetic microorganisms.

2. Charles Elton described biological communities in terms of feeding relationships, which he emphasized as a dominant organizing principle in community structure.

3. A. G. Tansley coined the term ecosystem to include the organisms and all the abiotic factors in a habitat.

4. Alfred J. Lotka provided a thermodynamic perspective on ecosystem function, showing that the movements and transformations of mass and energy conform to thermodynamic laws.

5. Raymond Lindeman, in 1942, popularized the idea of the ecosystem as an energy-transforming system.

6. The study of ecosystem energetics dominated ecology during the 1950s and 1960s, due largely to the influence of Eugene P. Odum, who championed energy as a common currency for describing ecosystem structure and function.

7. Gross primary production is the total energy assimilated by photosynthesis. Net primary production is the energy accumulated in plant biomass; hence it is gross primary production minus respiration.

8. Primary production can be measured by one or some combination of methods, such as harvesting, gas exchange (carbon dioxide in terrestrial habitats, oxygen in aquatic habitats), or assimilation of radioactive carbon (\(^{14}C\)).

9. Photosynthetic efficiency (gross production divided by total incident light energy) during daylight periods in the growing season is 1–2% in most habitats.
10. Because plants lose water in direct proportion to the amount of carbon dioxide they assimilate, plant production in dry environments is limited by, and varies with, the availability of water. Transpiration efficiency, also called water use efficiency, is the ratio of production (in grams of dry mass) to water transpired (in kilograms). Transpiration efficiency typically ranges between 1 and 2 g per kilogram; it occasionally reaches 4 g per kilogram in drought-adapted species.

11. Production in both terrestrial and aquatic environments can be enhanced by the addition of various nutrients, especially nitrogen and phosphorus, indicating that nutrient availability limits production. Stimulation of production by nutrients is greatest in systems where nutrient inputs are lowest.

12. Primary production of ecosystems is greatest in the humid Tropics. In other terrestrial environments, production is less, due to cold, dark, or drought. Among aquatic ecosystems, estuaries, coral reefs, and coastal algal beds are the most productive.

13. The movement of energy and materials through a food chain can be characterized by assimilation efficiency (the ratio of assimilation to digestion) and net production efficiency (the ratio of production to assimilation). Overall, the ecological efficiency of energy transfer from one trophic level to the next averages 5–20%.

14. Assimilation efficiency depends on the quality of the diet, particularly the amount of digestion-resistant structural material (cellulose, lignin, chitin, keratin) it contains. Assimilation efficiency varies from about 15% to 90%.

15. Material not assimilated is egested and becomes part of the detritus food chain.

16. Net production efficiency is lowest in animals whose costs of maintenance and activity are greatest, especially warm-blooded vertebrates. Typical net production efficiencies of 1–6% for warm-blooded vertebrates contrast with the values of 15–75% that are typical of invertebrates.

17. Gross production efficiency (the ratio of production to ingestion) varies from less than 1% up to 30%.

18. Exploitation efficiency measures the proportion of available food in a trophic level that is consumed by the next higher trophic level.

19. The average residence time of biomass or energy at a trophic level is the ratio of biomass, or of energy stored in biomass, to the rate of net production. Average residence times for primary production vary from 20 years in some forests to 20 days or less in aquatic, plankton-based communities.
Table 6.1  Rough estimates of food chain data from various field studies

<table>
<thead>
<tr>
<th>Community</th>
<th>Net primary production (kcal/m²/yr)</th>
<th>Consumer ingestion (kcal/m²/yr)</th>
<th>Ecological efficiency (%)</th>
<th>Number of trophic levels (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open ocean</td>
<td>500</td>
<td>0.1</td>
<td>25</td>
<td>7.1</td>
</tr>
<tr>
<td>Coastal marine</td>
<td>8,000</td>
<td>10.0</td>
<td>20</td>
<td>5.1</td>
</tr>
<tr>
<td>Temperate grassland</td>
<td>2,000</td>
<td>1.0</td>
<td>10</td>
<td>4.3</td>
</tr>
<tr>
<td>Tropical forest</td>
<td>8,000</td>
<td>10.0</td>
<td>5</td>
<td>3.2</td>
</tr>
</tbody>
</table>

Values are approximations based on many studies.

3. From the estimates presented in Table 6.1, what factor contributes most to variations in food chain length among ecosystems?

4. From the material in this and previous chapters, what biological factors account for variation in the factor you chose as your answer to Question 3?

5. Read the article from World Watch Magazine on Practicing Ecology on the Web at http://www.whfreeman.com/riekes about fishing down the food chain. What effects do you think overfishing will have on nutrient cycling and energy balance in the ocean?

Suggested Readings


