

ENERGY IN LIVING SYSTEMS

by

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The never-ending flow of energy within a cell, from one cell to another, and from one organism to another organism, is the very essence of life. Energy may be defined as the capacity to produce a change in matter. All changes in matter always involve some sort of energy exchange. This is true in living systems as well as non-living ones.

The cells of living things are characterized by the presence of complex, efficient systems such as chloroplasts and mitochondria which transform one kind of energy into another. The many chemical reactions of the cells which enable them to grow, move, maintain themselves, reproduce and respond to stimuli are collectively termed metabolism. The metabolic activities of bacterial, plant and animal cells are all remarkably similar despite the marked differences in their appearances. In most, if not all, cells glucose and other simple sugars are converted by way of a series of intermediate compounds to carbon dioxide and water. During these conversions, a part of the energy of the glucose molecule is conserved and made available to the cell to drive other processes.

Energy Transformations

The study of energy transformations in living organisms, termed "bioenergetics", is concerned with three major questions: (1) How do cells obtain biologically useful energy? (2) How do they utilize it in synthesizing their own cellular constituents? (3) How are these functions controlled so that they meet the moment-to-moment needs of the cells? We can distinguish three major types of energy transformations in the biological world (Figure 1). In the

first, the radiant energy of sunlight is captured by the green pigment, chlorophyll, present in the chloroplasts of green plants. Radiant energy is transformed by the process of photosynthesis into chemical energy which is used, in turn, to synthesize carbohydrates and many other complex molecules from carbon dioxide and water. The radiant energy of sunlight, a form of electromagnetic energy, is transformed into other forms of energy within the cells. The chemical energy is stored in the molecules of carbohydrates and other foods as the energy of the bonds which connect the constituent atoms.

The chemical energy of carbohydrates and other molecules undergoes a second type of energy transformation in the process termed "cellular respiration". The reactions of cellular respiration involving the step-by-step breakdown of glucose and other molecules occur primarily within the mitochondria and result in the production of energy-rich phosphate bonds. This makes the chemical energy available to drive the many functions of the cell.

When the chemical energy of the energy-rich phosphate bonds is utilized by cells to do work, a third type of energy transformation occurs. This may be the mechanical work of muscular contraction, the electrical work of conducting a nerve impulse, the osmotic work of moving molecules against a concentration gradient, or the chemical work of synthesizing new molecules for growth or for the storage of energy. As these transformations occur, energy finally flows to the environment and is dissipated as heat or thermal energy. Plants and animals have evolved not only some remarkably effective energy transducers (structures that can convert one form of energy into another) such as chloroplasts and mitochondria, but also some very effective control mechanisms to regulate the energy transducers and enable the cell to adapt its energy flow to variations in environmental conditions.

Thermodynamics

The branch of physics that deals with energy and its transformations is termed "thermodynamics". This consists of certain relatively simple, basic principles which are universally applicable to chemical processes whether these occur in living or nonliving systems. In all of these processes energy is neither created or destroyed, but is simply transformed from one form to another. The First Law of Thermodynamics may be stated as "energy may be changed from one form to another, but it is neither created nor destroyed." Alternatively, the first law may be stated as "the total energy of any system and its surroundings remains constant". The first law is sometimes called the Law of Conservation of Energy. As any system undergoes a change from its initial to its final state, it may absorb energy from the surroundings or deliver energy to the surroundings. The difference in the energy content of the system in its initial and final states must be just equaled by a corresponding change in the energy content of the surroundings. Energy can be exchanged as heat or as mechanical work. Heat is a means by which energy is exchanged between a system and its surroundings as a result of temperature differences. This is why the study of energy transfer involving heat has been termed "thermodynamics" (i.e., heat dynamics).

Nearly every physical or chemical event in both living and nonliving systems is accompanied by the exchange of heat with the surroundings. A process in which heat is delivered to the surroundings is said to be exothermic. A process in which heat is absorbed from the surroundings is termed endothermic. Although heat is an important and familiar means of transferring energy through temperature differences in man-made machines, it is not a useful way of transferring

energy in biological systems for the simple reason that living systems are isothermal. There is no significant temperature difference between different parts of the cell or between different cells in the body. Cells cannot act as heat engines because they have no mechanism for heat to flow from a warmer to a cooler body. Cells utilize the chemical energy in complex organic molecules to do work. The heat produced by cells is in part a waste product or it may serve to maintain a high body temperature in certain organisms.

The second law of thermodynamics may be stated briefly "in all processes in the universe the entropy increases". The concept of entropy can be used to predict whether a reaction can occur spontaneously. Entropy (S) is a measure of the degree of randomness or disorder of a system. The entropy of a system increases; that is, ΔS becomes positive as the system becomes more disordered. In almost all energy transformations some heat is lost to the surroundings. Since heat involves the random motion of molecules, such heat losses increase the entropy of the surroundings. Living organisms and their component cells are highly organized and thus have low entropy. They have been termed "islands of order in a vast sea of disorder". Living organisms preserve this low entropy by increasing the entropy of their surroundings. For example, people increase the entropy of their surroundings when they eat a candy bar and convert its glucose to carbon dioxide and water and return these molecules to the surroundings.

The force that drives all processes is this tendency to continuously increase the entropy by giving out or absorbing heat from the surroundings. Thus, the second law of thermodynamics may be rephrased; a process can occur spontaneously only if the sum of the entropies of the system and its surroundings

increases. The entropy of a system may decrease during a spontaneous process if the entropy of the surroundings increases enough so that the sum of the two is positive:

$$\Delta S_{\text{system}} + \Delta S_{\text{surroundings}} > 0 \quad (1)$$

The internal energy of a system is designated by the symbol E . This includes the translational, vibrational and rotational energies of the molecules plus the energy involved in chemical bonding and the energy involved in other nonbinding interactions between molecules. The internal energy is a function of the state of the system.

The term "enthalpy" (H) refers to the internal energy of the system (E) plus the product of its volume and the pressure exerted on the system: $H = E + PV$. Biological processes generally occur under conditions of constant pressure and if the pressure volume work ($W = p\Delta V$) is negligible, E and H are essentially the same.

Free Energy

Entropy is not a useful criterion of whether a biochemical process can proceed spontaneously because changes in entropy are not readily measured. The changes in heat and energy in a system are related by a third concept termed "free energy". This thermodynamic function, denoted by the symbol ΔG , ($G=H-TS$) was devised by Josiah Willard Gibbs over a century ago. This equation relates the change in free energy of a system, ΔG , to the change in enthalpy, ΔH , and the change in entropy, ΔS , when the absolute temperature, T , does not change. Since in biological systems, ΔE and ΔH are very similar, the equation may be written as $\Delta G \cong \Delta E - T \Delta S$. That is, the change in free energy, ΔG , depends

upon the change in internal energy and on the change in entropy of the system. The change in free energy of a system, ΔG , is a valuable criterion of whether the reaction can proceed spontaneously. A reaction can occur spontaneously only if ΔG is negative. The system is at equilibrium and no net change occurs if ΔG is zero. The reaction cannot occur spontaneously if ΔG is positive. Free energy may be visualized as that component of the total energy of a system that is available to do work under isothermal conditions. It is thus the thermodynamic parameter of greatest interest in biology. As entropy (S) increases during an irreversible process, the amount of free energy (G) decreases. All physical and chemical processes tend to proceed until they reach an equilibrium in which the free energy of the system is at a minimum and its entropy is at a maximum.

The ΔG of a reaction is the free energy of the final state, the products, minus the free energy of the initial state, the reactants. It is independent of both the path of the transformation and the mechanism of the reaction. The conversion of glucose to carbon dioxide and water, for example, has the same ΔG whether it occurs by combustion in a bomb calorimeter or by a long series of enzyme-catalyzed reactions in a living cell. Furthermore, the magnitude of the ΔG does not determine the rate of the reaction. The rate of the reaction depends on its energy of activation (E_a) which is not related to ΔG . Most chemical reactions are reversible, and this is indicated by the double arrow, \rightleftharpoons . The energy relations of the reactants and products, their relative concentrations, and their solubility are some of the factors that determine whether a reaction will occur and whether it will proceed from right to left or from left to right. The reaction, $A + B \rightleftharpoons C + D$ proceeds under a given set of conditions until it reaches an equilibrium point, at which there is no further net reaction and the relative concentrations of A, B, C and D remain unchanged. This is the point at which ΔG

equals zero. For each reaction, the thermodynamic equilibrium constant (K_{eq}) expresses the chemical equilibrium reached by the system:

$$K_{eq} = \frac{(C) \times (D)}{(A) \times (B)} .$$

The K_{eq} in general depends on P and T and is determined by the tendency of the reaction components to reach a state of maximum ~~energy~~^{entropy} or minimum free energy for the system. The equilibrium constant, K_{eq} , is related to the change in free energy of the components of the reaction: by $\Delta G^{\circ} = -RT \ln K_{eq}$. Where R is the gas constant (1.987 cal/mol degree), T is the absolute temperature, and $\ln K_{eq}$ the natural logarithm to the base e of the equilibrium constant. The symbol, ΔG° , represents the standard free energy change defined as the free energy change for the reaction under standard conditions when the reactants and products are present at concentrations of one molar.

The rate of a reaction is determined by a number of factors, among which are the temperature and the concentration of the reactants. The standard means of speeding up a chemical reaction in the laboratory is to supply energy to the system; e.g., applying heat to the molecules. This increases the motion of the atoms and molecules in the reaction mixture, increasing the probability that they will collide with enough energy to form an activated complex and react. Another way of increasing the rate of reaction is to increase the concentration of the reactants, which also increases the probability of collision between them. The law of mass action states that when all other conditions are constant, the rate of the reaction is proportional to the concentrations of the reactants. Reactions in biological systems are controlled primarily by the multitude of enzymes produced by the cell, each of which controls a specific reaction.

Catalysis

Many of the substances that are rapidly metabolized by living cells are remarkably inert outside the body. A glucose solution will keep indefinitely in the bottle if it is kept free of bacteria and molds. Glucose must be subjected to high temperature or to strong acids or bases before it will break down into its constituent atoms. Living cells obviously cannot use such extreme conditions to cleave glucose and instead utilize enzymes, protein catalysts produced by the cells. Since catalysts are not used up in the reactions, they can be used over and over again; a very small amount of catalyst will speed up the reaction of vast quantities of reactants. This is an efficient way of controlling the utilization of energy.

Even a strongly exoergic reaction which releases energy as it proceeds is prevented from beginning by an energy barrier termed "the activation energy". In any population of molecules some are relatively rich in energy, others are energy-poor. Only those molecules with a relatively high energy content are likely to react to form the product. One way to make the reaction go faster is to raise the energy of more of the molecules and overcome the activation energy barrier. This can be done by increasing the thermal energy; i.e., by heating the mixture, for the heat absorbed by the substance increases the molecular energy. They move faster, and this increases the likelihood that they will collide and react. Generally the speed of a chemical reaction doubles with every increase of 10°C in the temperature. Alternatively, the activation energy barrier can be decreased by the presence of a catalyst, which is the more appropriate alternative in biological systems.

A catalyst forms an unstable intermediate complex with the substrate which then decomposes to release the product and frees the catalyst to react

with a second molecule of substrate. This lowers the activation energy requirement of the reaction and allows a larger fraction of the population of molecules to react at any one time. The reduction of activation energy by the biological catalyst, the enzyme, permits the myriad reactions fundamental to life to occur. Each kind of enzyme regulates the speed and specificity of one or more of the thousands of chemical reactions that occur within the cells. Enzyme controlled reactions underlie all of the phenomena of life: respiration, muscle contraction, nerve conduction, photosynthesis, nitrogen fixation, deamination, digestion and so on.

The catalytic ability of some enzymes is truly phenomenal. One molecule of the iron containing enzyme, catalase from beef liver, will decompose 44,000 molecules of hydrogen peroxide (H_2O_2) each second at $0^\circ C$. Hydrogen peroxide is a poisonous substance that is produced as a byproduct in several enzyme reactions. Catalase protects cells by destroying the peroxide. Hydrogen peroxide can also be split by free iron atoms. However, iron accomplishes this only at a very slow rate. It would take 300 years for one iron atom to split the same number of molecules of H_2O_2 cleaved in one second by a molecule of catalase which contains one iron atom. This striking example of the evolution of a catalyst emphasizes one of the major characteristics of enzymes - they are very rapid and efficient catalysts.

Since many reactions release energy when going in one direction, it is obvious that to drive the reaction in the reverse direction the proper amount of energy in a useful form must be supplied.

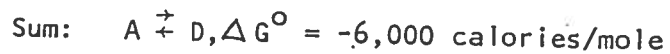
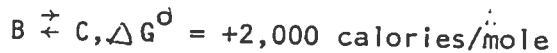
Coupled Reactions

To drive an energy-requiring (endoergic) reaction, some energy-yielding (exoergic) reaction must occur at about the same time. Two reactions that must

take place together so that one can furnish energy or one of the reactants needed by the other are termed "coupled reactions". In most biological systems energy-yielding reactions result in the synthesis of energy-rich phosphate bonds (ν P) such as the terminal bonds of adenosine triphosphate, ATP. The energy made available when these phosphate bonds are split by the addition of a molecule of water can then be used in a cell to conduct nerve impulses, contract muscles, synthesize proteins, and so on.

An important feature of thermodynamics is that the free energies (ΔG) of reactions are additive. In other words, the over-all change in the free energy, ΔG , of a series of reactions is equal to the sum of the changes in free energy of the individual steps. Because of this fact, a thermodynamically unfavorable reaction, one with a positive ΔG , can be driven by a thermodynamically favorable reaction, one with a negative ΔG , if the latter has greater value.

Consider the following sequence of reactions:



In this series, reactant A is converted to product D because the sum of the ΔG° is less than zero, even though one of the steps has a positive ΔG° .

Under standard conditions B is not converted to C because the ΔG° is positive.

The conversion of C to D is thermodynamically feasible, however, as is the conversion of A to B. Because the free energy changes of the sequence of reactions are additive, the conversion of A to D has a ΔG° of -6,000 calories/mole and can occur under standard conditions. Even though reaction $B \rightleftharpoons C$ would go

spontaneously from right to left, the preceding conversion of A to B increases the concentration of B and the following conversion of C to D decreases the concentration of C. Thus the conversion of A to B "pushes" reaction $B \rightleftharpoons C$ to the right while the conversion of C to D "pulls" it to the right. The two ^{exergonic} reactions combine to drive the ^{endergonic} reaction; the over-all free energy change in the sequence of reactions is less than zero. In any coupled system in which the sum of the free energy changes of the reactions is less than zero, reactants are converted to products and material flows from left to right. The number of reactions in the sequence, the number of starting materials, and the number of end products in any given reaction are all unimportant. Only one common intermediate between the two consecutive reactions is required in a coupled system. The nature of the common intermediate is also unimportant; it can be as simple as an electron or proton or as complex as a polypeptide or polynucleotide.

Enzymes usually work in teams, with the product of one enzyme-controlled reaction serving as the substrate for the next. We can picture the inside of a cell as a factory with many different assembly lines and disassembly lines operating simultaneously. In each assembly line one enzyme carries out one step such as changing molecule A into molecule B, and the next enzyme converts B to molecule C and so on. Germinating barley seeds contains two enzymes that convert starch to glucose. Amylase hydrolyzes starch to maltose and maltase splits maltose to glucose. Eleven different enzymes, working consecutively, are required to convert glucose to lactic acid. The same series of eleven enzymes is found in human cells, in green leaves, and in bacteria.

How does an enzyme work?

An enzyme can speed up only those reactions that will occur to some extent, however slight, in the absence of the enzyme. Many years ago the German chemist, Emil Fischer, suggested that the specific relationship of an enzyme with its substrate indicates that the two must fit together like a key in a lock. He suggested that the enzyme combines with its substrate to form an intermediate enzyme-substrate complex which then decomposes to release the enzyme and the product. This concept was formulated mathematically by Leonor Michaelis nearly 70 years ago. Michaelis assumed that such a complex does form and then calculated how the speed of the reaction should be affected by varying the concentrations of enzyme and substrate. Exactly those relationships which he predicted are observed experimentally. This is strong but indirect evidence that Michaelis' assumption that an enzyme-substrate complex forms as an intermediate in the reaction is correct.

Direct evidence of the existence of enzyme-substrate complexes was obtained by David Keilin of Cambridge University and by Britton Chance of the University of Pennsylvania. Chance isolated a brown-colored peroxidase from horseradishes. When he mixed this with hydrogen peroxide, a green-colored enzyme-substrate complex was formed. This was then changed to a second, pale red enzyme-substrate complex which finally cleaved to give the original brown enzyme plus the breakdown products of hydrogen peroxide; that is, water and oxygen. By measuring the changes of color with time Chance was able to calculate the rate of formation of the two successive enzyme substrate complexes and their rates of breakdown.

Only a relatively small part of the enzyme molecule combines with the substrate. This part is termed "the active site". The active site represents some special topographic feature of the enzyme, usually a cleft or a groove on its surface into which the substrate or some portion of it fits. Biochemists have been able to locate the active site of many enzymes and to identify the specific amino acids present at the active site.

Although it is clear that enzymes reduce the activation energy needed for a reaction to begin so that the substrate is much more reactive when it is part of an enzyme-substrate complex than when it is free, it is not clear why this should be true. One theory postulates that the enzyme unites with the substrate at two or more points, holding the substrate in a position which strains its molecular bonds and makes them more likely to break. The enzyme-substrate complex is typically bonded by weak bonds such as ionic, hydrogen, hydrophobic and van der Waal's forces; a few enzyme-substrate bonds involve covalent binding.

Factors Affecting Enzyme Activity

The activity and specificity of an enzyme depend upon its molecular conformation; that is, upon its tertiary and quaternary structure. Thus, it follows that enzyme activity is reduced or abolished by any factor that changes the molecular conformation. These include thermal energy, changes in pH, and the presence of heavy metals such as lead.

Enzymes are inactivated by high temperatures. Below the temperature at which an enzyme is inactivated the rates of most enzyme controlled reactions,

like the rates of chemical reactions in general, are doubled by each increase of 10°C .

The activity of an enzyme is markedly changed by changes in the acidity or alkalinity of the reaction median. Most of the enzymes that operate within cells have pH optima near neutrality and will not work well when the medium is made acid or alkaline. Stronger acids or bases irreversibly inactivate enzymes by permanently changing their molecular conformation.

If the pH and temperature of an enzyme system are kept constant and if an excess of substrate is present, the rate of the reaction is directly proportional to the amount of enzyme present. If the pH, temperature and enzyme concentration of the system are kept constant, the initial rate of reaction is proportional to the amount of substrate present up to a limiting value. Since enzymes catalyze the attaining of equilibrium from either direction, what we usually consider to be the product of the reaction is also a substrate for the reverse reaction. It, too, binds to the enzyme at its active site. Thus, as a reaction proceeds and the substrate is converted to product, the accumulating product may bind to the enzyme (thereby decreasing the number of enzyme molecules available to bind with substrate) and decrease the rate of the forward reaction.

Adenosine Triphosphate: the primary energy currency of the cell

All of the phenomena of life - growth, movement, irritability, reproduction - require the expenditure of energy by the cell and a corresponding continued input of free energy. Cells utilize free energy for the synthesis of substances from simpler precursors, for the active transport of molecules and ions across membranes,

and for the performance of mechanical work such as the contraction of muscle and the beating of cilia. Free energy is used to maintain the organism in a state that is far from equilibrium, with a minimum of entropy and a maximum of free energy. Plants derive free energy from the radiant energy trapped in photosynthesis. Animals and other heterotrophs such as fungi derive it from the oxidation of foodstuffs. The free energy obtained is stored in a special carrier of free energy, adenosine triphosphate (ATP).

The biologic problem of combining markedly exoergic reactions, such as the oxidation of glucose, with tremendously endoergic reactions, such as the synthesis of a peptide from amino acids, was solved by modifying both reactions so that they have a common intermediate, a compound produced by one and used by the other, ATP. The exoergic cleavage of ATP converts an otherwise endoergic synthesis of peptides into an over-all exoergic reaction. In the oxidation of glucose, the resynthesis of ATP (and of guanosine triphosphate - GTP) used in peptide synthesis permits the synthesis of peptides to be driven by the oxidation of glucose. A markedly exoergic process, the oxidation of glucose, is modified so that nucleoside diphosphates and monophosphates are phosphorylated to form nucleoside triphosphates. This decreases the liberation of free energy that would otherwise accompany the oxidation of glucose. The nucleoside triphosphates are then used in endoergic processes and are cleaved in these reactions to diphosphates and monophosphates. Although the overall effect is that of a direct transfer of energy, the biochemical mechanism involved is a coupling of exoergic and endoergic reactions in which the nucleoside triphosphates serve as energy carriers.

ATP is an energy-rich molecule because its triphosphate moiety contains two phosphoanhydride bonds. A large amount of free energy is liberated when ATP is hydrolyzed to adenosine diphosphate (ADP) and inorganic phosphate (P_i) or

to adenosine monophosphate (AMP) and pyrophosphate (PP_i). In contrast, the hydrolysis of the phosphate of AMP to form free adenosine yields much less free energy. This reaction is the hydrolysis of a phosphate ester, the splitting of a bond between an alcohol group in adenosine and the acid group of phosphoric acid. The hydrolysis of ATP or ADP represents the cleavage of an oxygen bridge between two phosphorus atoms, the cleavage of a phosphoanhydride bond, which is a reaction with a high standard free energy change. For this reason, such bonds and the compounds that contain them have been termed energy-rich or high energy bonds and compounds.

Because the free energy of hydrolysis is not localized in the covalent bond joining the phosphorus atom to the oxygen atom, the term "energy-rich phosphate bond" is actually a misnomer. Despite this, it is a very useful term deeply ingrained in biochemical thought by long usage. The term simply implies that the bond or compound has a large standard free energy of hydrolysis, although the free energy change is the result of changes in the chemical potential of all the components of the system, including water and the hydrogen ion. Bonds are chemically designated with a \sim symbol if their cleavage by hydrolysis produces a large negative standard free energy change. ATP may be written A-P \sim P \sim P because the two terminal phosphate bonds are energy-rich anhydrides whereas the bond between the adenosine and the first phosphorus is an ordinary ester bond.

Some biosynthetic reactions are driven by other nucleoside triphosphates such as guanosine triphosphate, GTP, uridine triphosphate, UTP, and cytidine triphosphate (CTP).

Solar Energy

Humans and other animals derive their energy from the foodstuffs that they eat. Our fruits and vegetables are derived directly from plants, but our

meat, fish and shellfish are products of animals. These animals, in turn, derive their energy supply from the plants that they eat (Figure 2). Ultimately all of the food and energy of the animal world comes from the plant world. Green plants require for growth only water, carbon dioxide, nutrient salts, and an abundant supply of the radiant energy from the sun. Solar radiation is the ultimate source of the vast majority of the biological energy on this planet. At the very high temperatures (about 10 million degrees C) that occur in the interior of the sun protons are transformed by thermonuclear reactions to helium nuclei with the release of energy mostly in the form of gamma rays (electromagnetic radiation). The gamma rays react with electrons and atoms in the surface of the sun and the energy is ultimately emitted as photons of lower energy (infrared, light, ultraviolet) which pass out of the sun.

The total amount of energy arriving at the earth from the sun is about 13×10^{23} kilocalories (or about 2×10^7 kW per year (Figure 3). The amount of solar energy reaching the earth each day is roughly equivalent to a million atom bombs of the size used in World War II. About one-third of this solar energy is reflected back into space from the surface of the earth as light. Much of the remaining two-thirds is absorbed by the earth and converted to thermal energy. Some of this absorbed energy is utilized to evaporate the waters of seas and lakes, producing clouds that fall as rain. Solar energy is one of the factors responsible for the movements of air and water that influence the patterns of climate all over the earth.

Only a small fraction of the solar energy reaching the earth is utilized by plants in photosynthesis and thus becomes available to drive all the processes of life. Large areas of the earth have no plants. Plants can utilize

in photosynthesis only some 3 per cent of the solar energy falling on them. The radiant energy is converted into the energy of the chemical bonds of the organic substances synthesized by the plant. When an animal eats a plant, or when bacteria decompose it, these organic substances are oxidized. The energy liberated is just equal to the amount of energy used in synthesizing the substances (First Law of Thermodynamics). However, some of the energy is transferred back to the environment as heat and not useful (free) energy (Second Law of Thermodynamics). Consequently, the entropy of the system increases. When the animal in turn is eaten by another animal, a further decrease in free energy occurs as the second animal oxidizes the organic substances of the first to liberate energy and synthesize its own cellular constituents. Eventually all the radiant energy originally trapped by plants in photosynthesis is transferred as heat and dissipated back to outer space.

The total amount of carbon incorporated into organic compounds by all the plants on the earth and in the waters of the globe is estimated to be some 200 billion (2×10^{11}) tons each year. Land plants synthesize about one-tenth of the total and marine plants and microscopic algae synthesize the remainder. The formation of each mole of glucose--180 grams--requires the input of 686 kilocal of about 3×10^{16} J. of radiant energy. To simplify calculations, let us assume that all of the 2×10^{11} tons of carbon are fixed in the form of glucose. This would require some 2×10^{18} kilocal of solar energy. If we make corrections for frictional losses in the process, our estimate of the total flux of biological energy ~~faces~~^{fixes} perhaps another hundred-fold, to 2×10^{20} kilocal of solar energy captured per year. This is only about one-thousandth of the total solar energy (about 12×10^{23} kilocal) that is estimated to fall on the earth in the course

of a year. The activities of green plants lead to a renewal of all the carbon dioxide in the atmosphere and dissolved in the waters of the world every 300 years and a renewal of all the oxygen in the atmosphere in about 2,000 years.

The total mass of all the organisms that have lived on the earth in the past two or three billion years is much greater than the mass of carbon and nitrogen atoms present on the planet. The Law of the Conservation of Matter assures us that matter is neither created nor destroyed. Obviously, the carbon and nitrogen atoms must have been used over and over again in the formation of new generations of plants and animals. The earth neither receives any great amount of matter from other parts of the universe nor does it lose significant amounts of matter to outer space. The atoms of carbon, hydrogen, oxygen, nitrogen, phosphorus and the rest are taken from the environment, made a part of some cellular component and finally, perhaps by quite a circuitous route involving several other organisms, are returned to the environment to be used again. Green plants, animals, fungi and bacteria all play roles in this cyclic use of the elements..

Energy Flux

The cycles of the elements are closed: the atoms are used over and over again. To keep the cycles going does not require new matter, but it does require energy, for the energy cycle is open rather than closed. As stated in the Second Law of Thermodynamics, whenever energy is transformed from one kind to another, there is an increase in entropy and a decrease in the amount of useful energy. Some energy is degraded and dissipated as heat.

Only a small fraction of the solar energy reaching the earth is trapped; considerable areas of the earth have no plants, and plants can utilize in photosynthesis only about 3 per cent of the incident energy. This radiant energy is converted into the energy of the chemical bonds of the organic substances made by the plant. When an animal eats a plant, or when bacteria decompose it, and these organic substances of the plant are oxidized, the energy liberated is just equal to the amount of energy used in synthesizing the substances (First Law), but some of the energy is released as heat and not as useful energy (Second Law of Thermodynamics). If this animal is eaten by another animal, a further decrease in useful energy occurs as the second animal oxidizes the organic substances of the first to liberate energy to synthesize its own cellular constituents. Since in these successive transfers one organism serves as the food of another, the overall chain of energy transfer is called a food chain. We can distinguish three types of food chains, a predator chain, a parasite chain, and a saprophyte chain. Many food chains operate simultaneously and interlock so that the total pattern is called a food web (Fig. 4).

Food Chains and Food Webs

The transfer of energy through a biological community begins with the capture of the radiant energy of the sun in the process of photosynthesis. As we have seen, only eight per cent of the sun's energy reaching this planet strikes plants and of this only some three per cent is utilized in photosynthesis. Part of this accumulation of energy, termed the primary production, is utilized by the plant for its metabolic processes, the remainder is stored and expressed as growth, the net primary production. The net primary production of a stand of pine trees is about 1.3 per cent of the radiant energy of the sun falling

on the trees. Tropical forests and sugar cane fields have net primary production rates of about two per cent of the radiant energy of the sun striking them.

The stored energy accumulates as biomass, the total mass of the organisms. Part of the biomass is cycled seasonally by death and decomposition; the rest, remaining alive, is the standing crop biomass. As you might expect, this can vary with the season. Grasslands undergo an annual turnover, but in forests energy is tied up for long periods of time in wood. In terms of energy the most productive ecosystems are coral reefs and estuaries; the least productive, deserts and the open ocean beyond the continental shelves. The available evidence suggests that the production of plant material in each area has reached an optimum level limited only by climate and soil.

The consumers depend upon the net production of the green plants. Not all of the net production available to herbivores is assimilated. A grasshopper assimilates only 30 per cent of its food; some mice assimilate as much as 90 per cent of their food. The energy of the assimilated food is utilized in keeping the herbivore alive and much is eventually lost as heat. The residue, stored in the form of new tissues and new individuals, is available to the carnivore that eventually eats the herbivore.

Ecological Pyramids

Various kinds of graphic representations have been employed by ecologists to illustrate the trophic structure of biological communities. There are three kinds of ecological pyramids: the pyramid of numbers, the pyramid of biomass and the pyramid of energy flow (Fig. 5). The pyramid of numbers owes its geometry to the fact that a great many small units are required to equal the

mass of one big unit. Since energy is dissipated at each link in the food chain much less is available at the higher levels. In addition, small organisms usually have faster metabolic rates than larger ones. The pyramid of biomass better illustrates the quantitative relations of the standing crops. When the total weight of the individuals at any one moment at successive trophic levels is plotted, a gradually sloping pyramid is obtained as long as there is no very great difference in size in the various organisms. If, however, organisms at the lower levels are very much smaller than those at the higher levels the pyramid may be inverted. The rapid metabolism and turnover of the smaller organisms accomplish a larger output of energy with a smaller standing crop biomass. In short, the number and mass of organisms supported at any level depends upon the rate at which food is being produced.

The pyramid of energy flow gives the best picture of the functional nature of communities. Whereas the other pyramids depict the situation at a given moment, the energy pyramid expresses the rates at which food passes through the food chain. From knowledge of the energy pattern it is possible to calculate the standing crop and the number of individuals the community will contain if one knows in addition the mean mass of individuals and their mean life span.

Some animals eat but one kind of food and, therefore, are members of a single food chain. Other animals eat many different kinds of food and not only are members of different food chains but also may occupy different positions in different food chains. An animal may be a primary consumer in one, eating green plants, but a secondary or tertiary consumer in others, eating herbivorous animals or other carnivores (Fig. 6).

Human beings are at the end of a number of food chains. We eat a fish such as a black bass, which ate little fish, which ate small invertebrates, which ate algae. The ultimate size of the human population, or of the population of any animal, is limited by the length of the food chain, the per cent efficiency of energy transfer at each step in the chain, and the amount of solar energy falling on the earth.

Since humans can do nothing about increasing the amount of incident solar energy and very little about the per cent efficiency of energy transfer, we can increase our food energy only by shortening the food chain; that is, by eating the primary producers, plants, rather than animals. In overcrowded countries people are largely vegetarians because this food chain is the shortest and a given area of land can in this way support the greatest number of people. Steak is a luxury in both ecologic and economic terms, but hamburger is just as much an ecologic luxury as steak is.

There is a loss of energy, and hence a smaller biomass, at each step in a food chain. H. T. Odum has calculated that 8100 kg. of alfalfa plants are required to provide the food for 1000 kg. of calves, which provide enough food to keep one 12-year old, 48 kg boy alive for one year. Although boys eat many things other than veal and calves other things besides alfalfa, these numbers illustrate the principle of a food chain and the pyramid of numbers. One boy required 4.5 calves per year to eat and these, in turn, require some 20,000,000 alfalfa plants as food.

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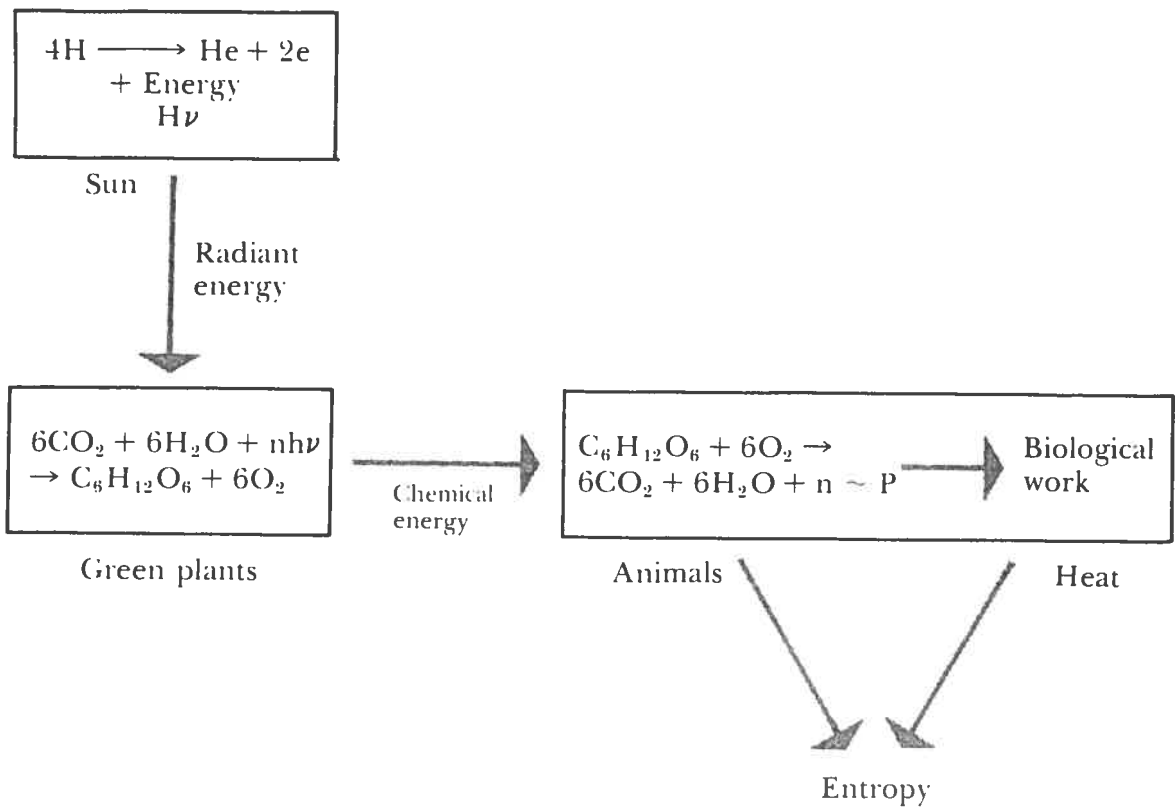


Figure 1. Types of energy transformations in the biological world: Photosynthesis, cellular ^{respiration} ~~reproduction~~ and biological work.

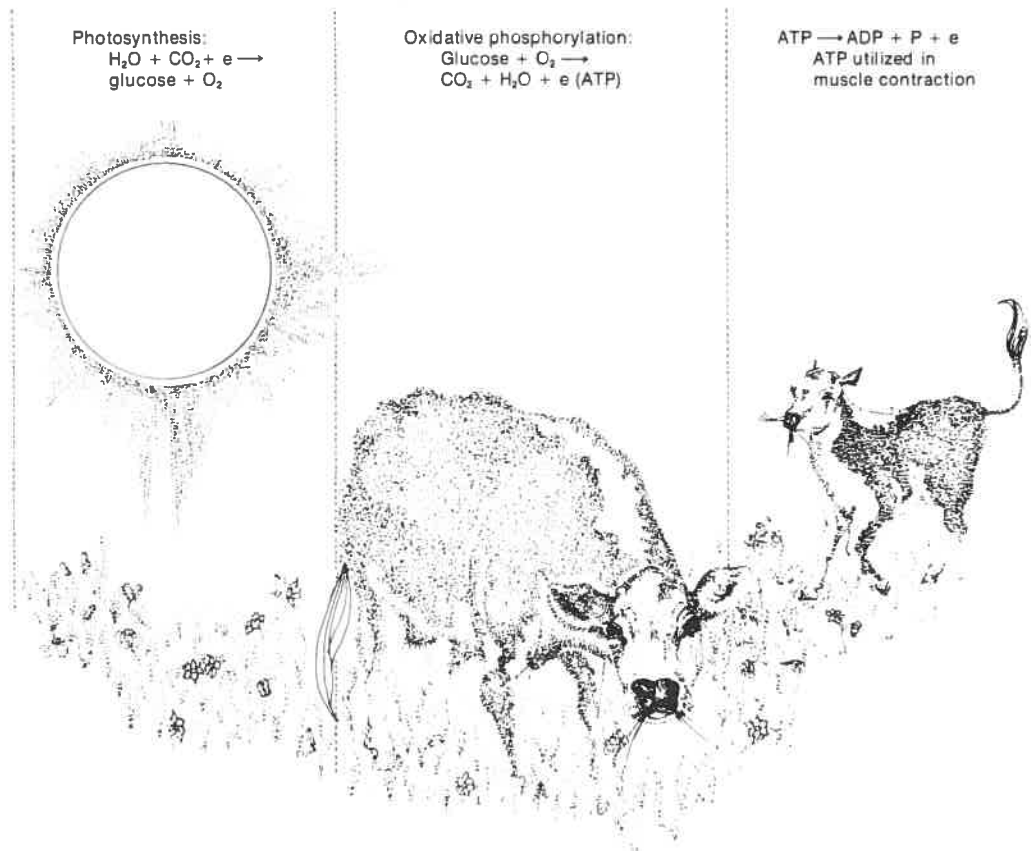


Figure 2. The flow of energy from sunlight through green plants to animals.

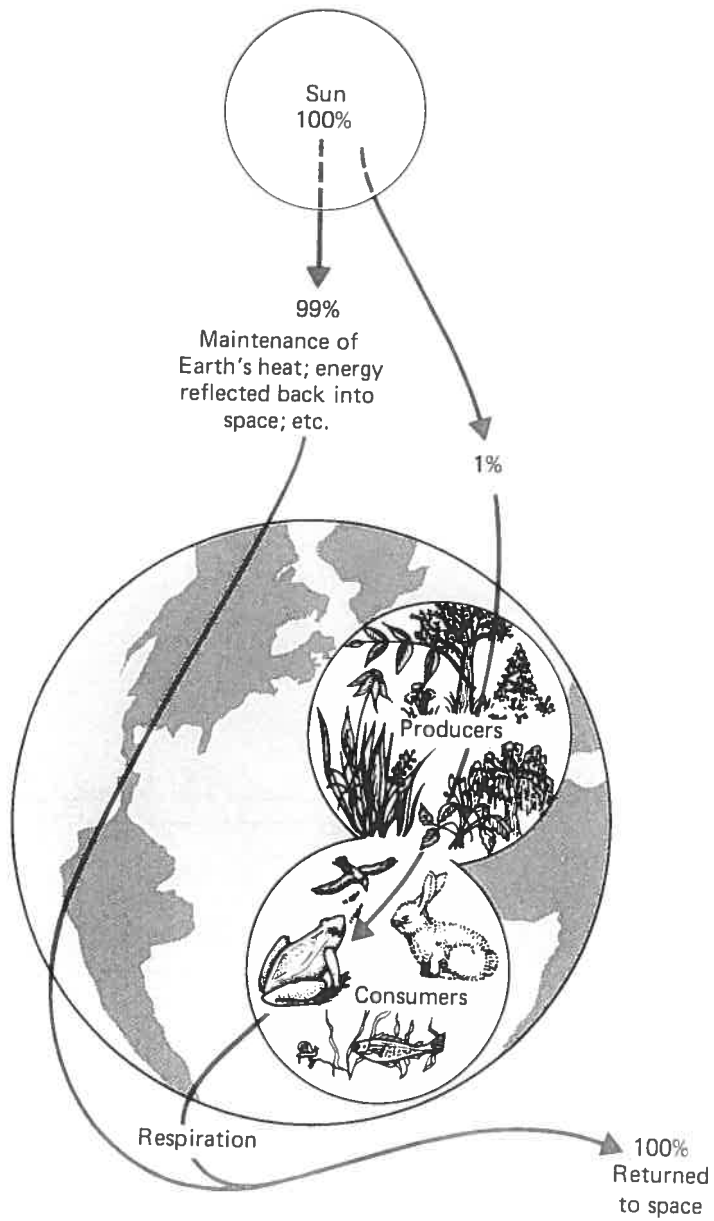


Figure 3. Utilization of solar energy on the earth.

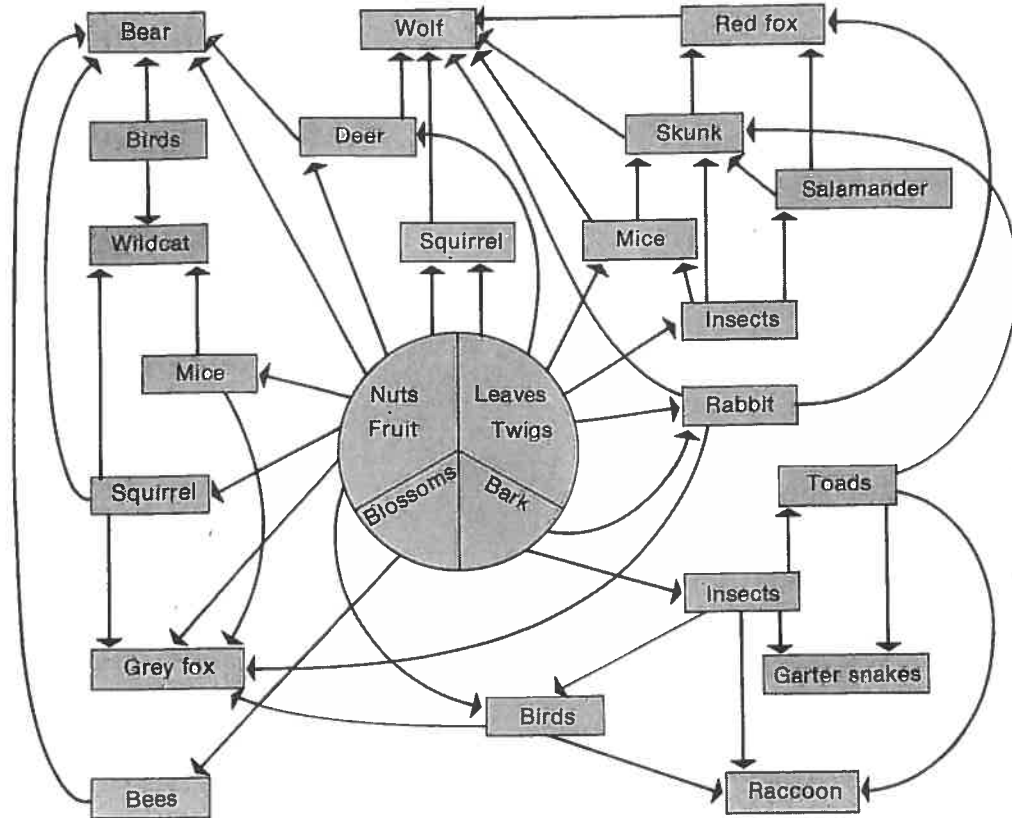


Figure 4. An example of a food web, composed of many interlocking food chains.

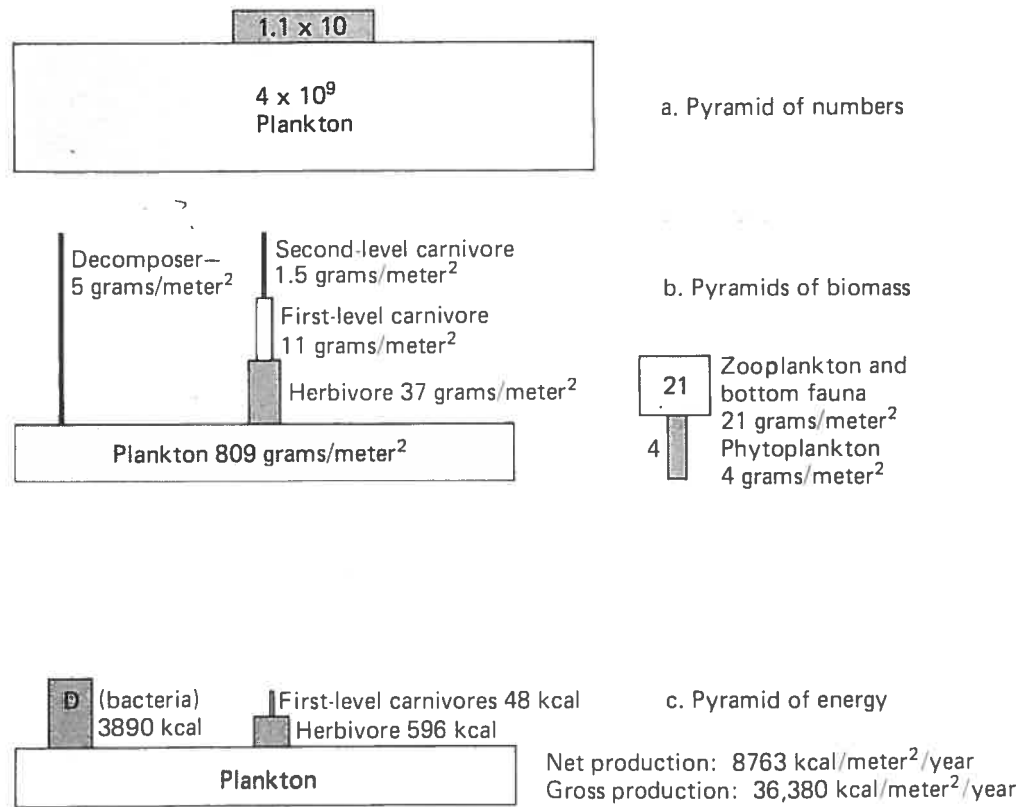


Figure 5. Types of ecological pyramids: (a) pyramid of numbers, (b) pyramid of biomass, (c) pyramid of energy

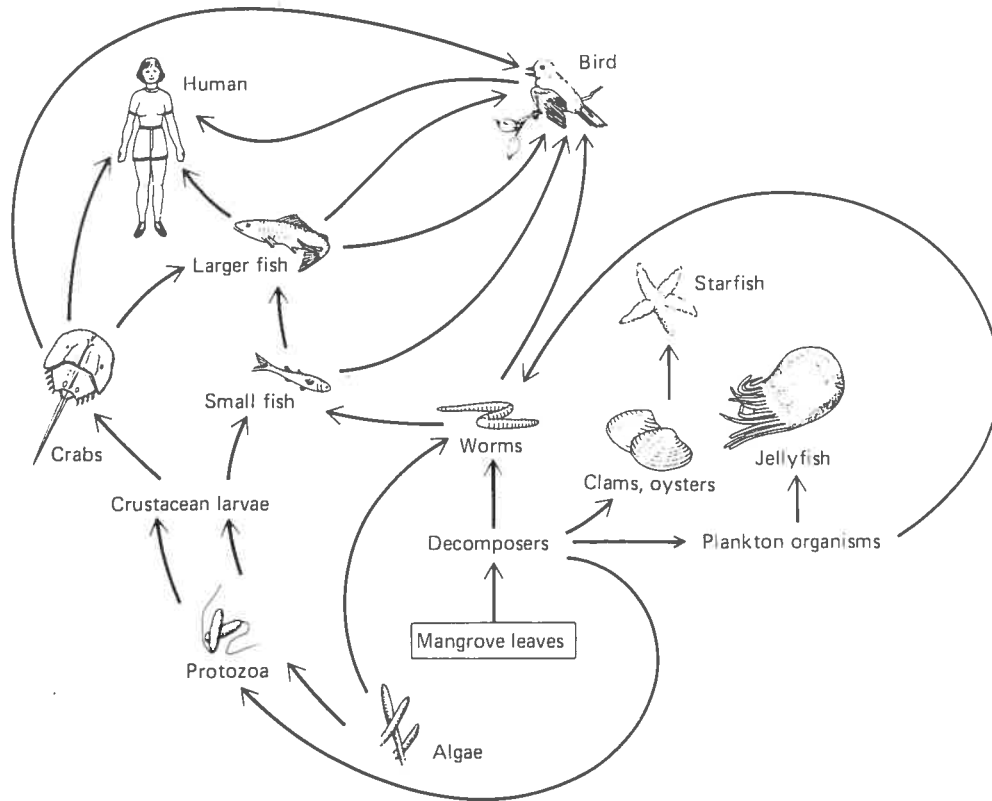


Figure 6. Human beings stand at the end of many food chains, a few of which are indicated in this diagram.