生态学原理

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Principles of Ecology

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Chapter 4

COMMUNITY AND ECOSYSTEM ECOLOGY: INTERACTIONS AND ORGANIZATION

TYPES OF INTERACTIONS

One of the first ecological observations to be recorded was that organisms live in ***communities.*** Certain species live together in a certain habitat and this combination of species tends to recur, more or less exactly, as the habitat recurs, with habitat and organisms bound together by interactions. This interacting system of community plus habitat is known as the ***ecosystem,*** a term first used by the English plant ecologist Sir Arthur Tansley.

F. E. Clements used three terms to describe the interactions between organisms and environment: *action, reaction,* and *coaction.* The environment *acts* upon the organisms of the community in many ways (see Chap. 2), including all the effects of temperature, wind, light, humidity, and soil moisture on the community.

The organisms of the community also *react* upon their environment. This meaning of the term ***reaction,*** the effects of organisms upon their physical environment, occurs only in ecology. Visualize a large area of bare dirt, perhaps a construction site, and then consider how it would be different if a forest, including not just trees but smaller plants, animals, and microorganisms, were suddenly there. The community would produce shade so that the light intensity would be lowered and temperatures would be moderated. The trees would act as barriers to wind and sound. As leaves fell and earthworms tunneled soil would be built. Plant leaves would intercept rainfall and allow it to reevaporate, and humus would soak up water so that runoff and erosion would be lessened. These effects are all reactions produced by a forest. The organisms of grasslands, lakes, and other communities produce their own reactions.

In an earlier section we defined *pollution* as the unfavorable modification of the environment as a by-product of man's activities. This is the same as saying that pollution consists of man's reactions. In this sense, pollution is a natural activity. However, man's reaction upon his environment has become a serious matter for the whole world for three reasons: (1) man has become a cosmopolitan species, occurring over the whole surface of the globe; no other species is so widely distributed; (2) humans are large both in physical size and in numbers; and (3) by utilizing energy subsidies, mainly from fossil fuel, man can exert effects (produce reactions) on the environment many times greater than a comparable animal which uses only the energy from its own metabolism.

The third kind of ecosystem interaction is ***coaction***, the effect an organism has on another. One organism feeds on another and is in turn eaten by a third, setting up a food chain. An insect obtains food from a flower and thereby pollinates it. Rabbits crop off certain kinds of trees but leave black cherries, which grow up to dominate a field. Coactions may be as general as a tree limb serving as a site for a bird nest, or as specific as the relationship between the fig tree and its single pollinator, the Blastophaga wasp.

We have mentioned several types of coactions and discussed three, predation, disease, and competition (Chap. 3). Some other types of coactions are parasitism, commensalism, and mutualism.

Predation, Parasitism, and Disease. **Predators, parasites,** and **pathogens** all make a living at the expense of other organisms, their prey or hosts. Predators usually kill and eat their prey, which are about the same size or smaller than the predators. Parasites are generally small in comparison to their host and do not kill and eat it but obtain their food from body fluids or in some other nonfatal way (if the host is not too heavily infested and is otherwise healthy). Pathogens are microorganisms, usually bacteria or viruses, that sicken the host by living within it.

Anyone would identify a tiger, a tapeworm, and a polio virus as predator, parasite, and pathogen, respectively. However, there are interactions that are as much predation as parasitism and others that are as much parasitism as disease. Furthermore, there is no clear dividing line between parasites and disease organisms, on the one hand, and organisms that are a normal part of the body's flora and fauna, called ***commensals***, on the other.

Commensalism. Commensals may be microorganisms such as the coliform bacteria that live in your intestine, slightly larger such as the mites that live in the oil glands around your nose, or ordinary-sized animals such as the house mice and house sparrows that live in or on your house rather than in or on you. Individuals of commensal species gain some advantage from the relationship; the effect is neutral for individuals of the other species. Other examples of commensalism not involving man are the use of prairie dog holes as nest sites for the burrowing owl and the use of old bird nests as nest sites for deer mice. A favorite textbook example is the remora, a fish with a suction cup on the top of its head, by which it attaches itself to a shark. It thus travels with the shark and eats the leftover scraps.

Mutualism. The dividing line between commensalism and mutualism is also unclear. Both individuals benefit from the association in mutualism. The usual example is the association of alga and fungus to form a lichen, but there are many others just as good. The relationship between termites which, like most organisms, cannot digest wood and the protozoans that live in their gut and can, is mutualism. So is the relationship between the rhinoceros and the tickbird, which rides around eating ticks and other insects off the rhinoceros.

The word *symbiosis* has sometimes been used to describe the relationship here termed mutualism. Symbiosis comes from roots meaning "to live together" so that, logically, it encompasses all coactions involving a continued, intimate association.

Action, reaction, and coaction are the bases for the structure and functioning of the community and the ecosystem. The structural and functional traits unique to this level of organization are the subjects of this and the following chapter.

ENERGY IN ECOSYSTEMS

TROPHIC STRUCTURE AND THE FOOD CHAIN

The word *trophic* means "feeding." The trophic structure of communities is based on the *food chain*, the sequence of organisms in which one organism feeds on the one preceding it. A typical food chain might be oak leaf → caterpillar → scarlet tanager → Cooper's hawk. In most communities several or many food chains exist which have interconnections at different points, forming a *food web*. The food web for most communities is very complex, involving hundreds or thousands of kinds of organisms (Fig. 4–1). One useful simplification is to group organisms into categories known as *trophic levels*, based on their position in the food chain (Fig. 4–2). The major categories are producers, consumers, and decomposers.

Producers. Producers (also called *autotrophs*) are organisms that can make food from simple inorganic materials. By *food* we mean complex organic compounds such as carbohydrates, fats, and proteins. Green plants are the producers with which most of us are familiar, and their food-making process is *photosynthesis*. In this process (see Chap. 2) plants use carbon dioxide, water, and some minerals, first, to produce carbohydrates and later various other organic materials, with oxygen being given off. Energy is as important as the materials involved. In the pho-

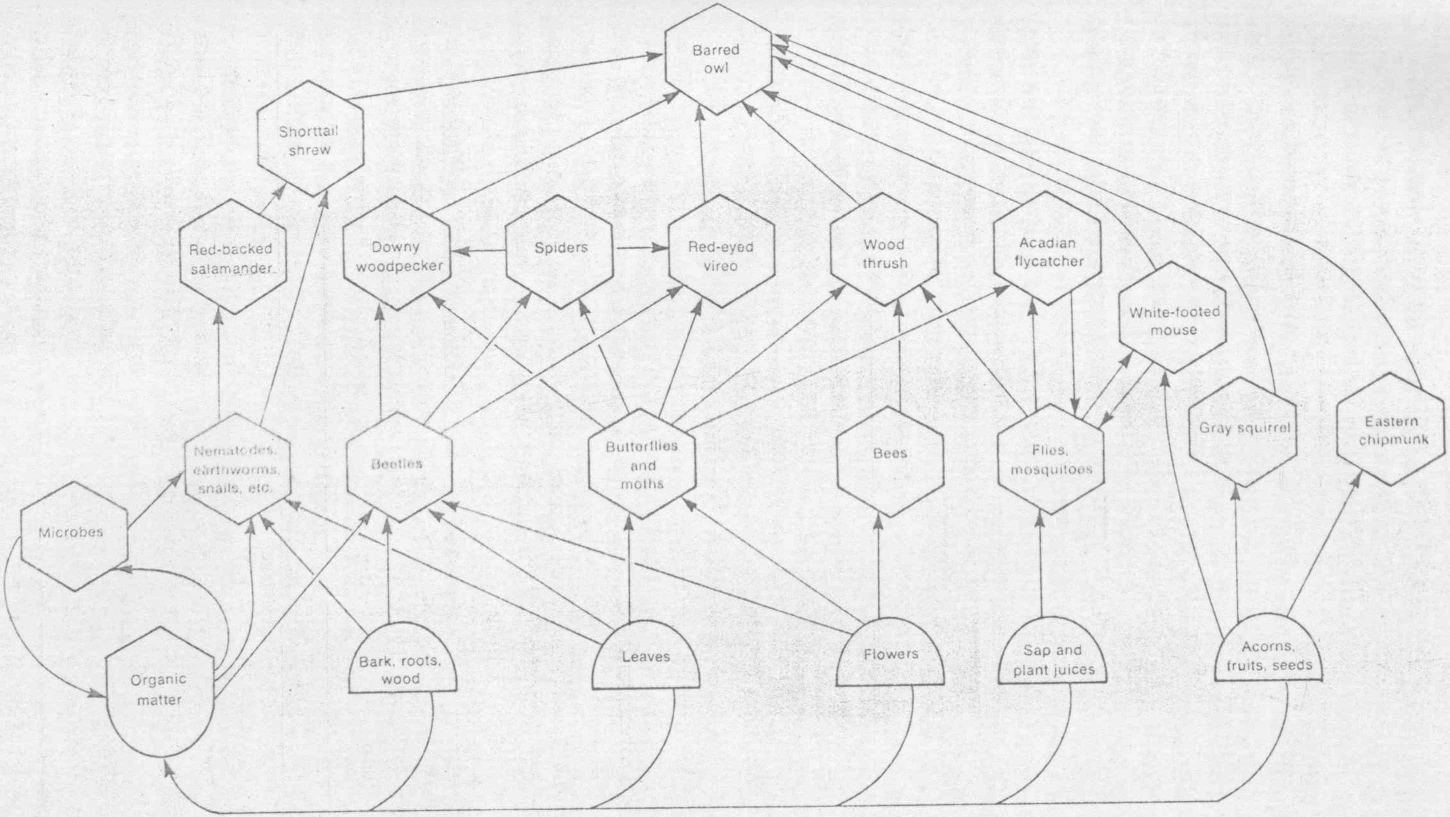

Figure 4–1. This food web for deciduous forest is greatly simplified as compared to the actual situation. Tens or hundreds of species have been lumped together in such categories as "beetles" and "nematodes, earthworms, snails, etc." Many species have been omitted, such as nuthatches, turtles, and fleas. Many connections are not shown. For example, mosquitoes bite other kinds of mammals in addition to mice, and other birds besides Acadian flycatchers eat mosquitoes. All of the animals provide food for the microbes. Despite these simplifications, the food web is still too complicated to comprehend easily. By grouping species into trophic catogories, the situation becomes somewhat clearer.

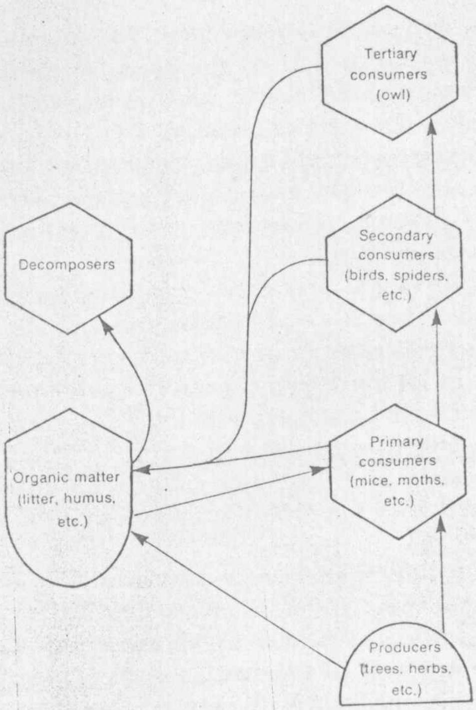

Figure 4–2. Here organisms of the deciduous forest are grouped into trophic levels based on the number of links that precede them in the food chain. All of the photosynthetic plants are in one trophic level, the producer level; all the organisms that eat mainly plants are in the primary consumer trophic level, etc.

tosynthetic process the radiant energy of sunlight is converted to chemical energy and stored in the chemical bonds of the compounds made by the plants.

Consumers. These are organisms that obtain their food by consuming other organisms. If they consume plants they are called *herbivores*, or *primary consumers*. If they obtain their food from green plants indirectly, by eating other animals, they are called *carnivores*, or *secondary* and *tertiary* consumers. All organisms other than autotrophs, those that have to get at least some of their foods prefabricated, are known as *heterotrophs*.

All animals are heterotrophs, as are fungi and most types of bacteria. We are most familiar with larger heterotrophs such as ourselves (or frogs or rats) that eat food, break it down partially in their digestive tracts, and absorb it mainly into the blood. The organic compounds from the bloodstream are absorbed by various cells in the body, where these compounds are used in two principal ways. They may be used as building blocks for other compounds or for new cells or they may be broken down to yield energy.

The latter process is *respiration*, in which organic compounds are combined with oxygen; the stored energy is released and carbon dioxide, water, and some mineral wastes are formed. The energy is that used by the organism for all its work—such as repairing and constructing cells, moving around, courting, fighting, and catching more food. The energy used for these functions is then given off as heat by the organism into the environment. Most of the carbon dioxide, water, and minerals resulting from respiration are *excreted* in one form or another.

Respiration is a universal process; every organism, heterotroph or autotroph, including green plants, respires. The energy that a plant uses for its work, such as growing and flowering, comes from the respiration of foods previously produced by photosynthesis.

Decomposers. These include scavengers and decay organisms such as fungi and many kinds of bacteria. They use dead plants and animals and excreta as their food source. The processes of digestion, respiration, and excretion are basically similar in all kinds of heterotrophs whether they are animals, bacteria, or fungi. Decay bacteria secrete their digestive enzymes into dead material outside their own bodies and absorb the food molecules rather than biting off a chunk and digesting it internally but these are really only details compared with the difference between autotrophy and heterotrophy.

If we go to the trouble to count the number of organisms in different trophic levels, we sometimes find that there are more plants than herbivores and more herbivores than carnivores, a pattern called the *pyramid of numbers*. A similar pattern, the *pyramid of biomass*, almost always results if dry weight is used instead of numbers. The pyramids of biomass

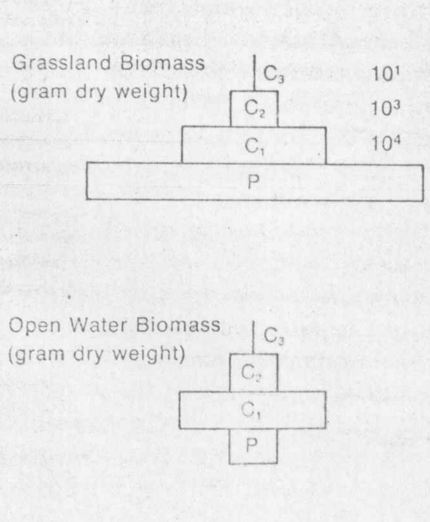

Figure 4–3. At the top are pyramids of numbers and of biomass (weight) such as might be expected in a thousand square meters of temperate grassland. C_1 = primary consumers, C_2 = secondary consumers, C_3 = tertiary consumers, and P = producers. There may be millions of grass plants, hundreds of thousands of grasshoppers, aphids, etc., thousands of carnivores such as spiders, and a few top carnivores like hawks or badgers. The pyramid in the middle represents the same situation but weight (specifically oven-dry weight) is used instead of numbers. The plants in a thousand square meters may weigh hundreds of thousands of grams, the primary consumers may weigh thousands of grams, etc. The third drawing, at the bottom, shows biomass by trophic level that does not form a pyramid. This sometimes occurs in open water of lakes or oceans where the producers are small and reproduce rapidly (single-celled algae, for example) and the consumers are large and long-lived (fish or large invertebrates).

and numbers are aspects of the structure of the ecosystem (Fig. 4–3). The functional basis of the pattern is in the flow of energy in the ecosystem.

ENERGY FLOW IN THE ECOSYSTEM

About 30% of the sunlight reaching the earth's atmosphere is reflected back into space, about 50% is absorbed as heat by ground, vegetation, or water, and about 20% is absorbed by the atmosphere, which does not seem to leave much for photosynthesis. In fact, only about 0.02% of the sunlight reaching the atmosphere is used in photosynthesis. Nevertheless, it is this small fraction on which all the organisms of the ecosystem depend.

Let us trace the path of energy in the community (Fig. 4–4). Of the energy stored in organic compounds in photosynthesis, the green plants themselves use some in respiration for their own growth and maintenance, with this energy being given off as heat to the surroundings. Primary consumers, or herbivores, eat plants. Some of the energy obtained in this way is stored in the growth of new tissue (and, in reproduction,

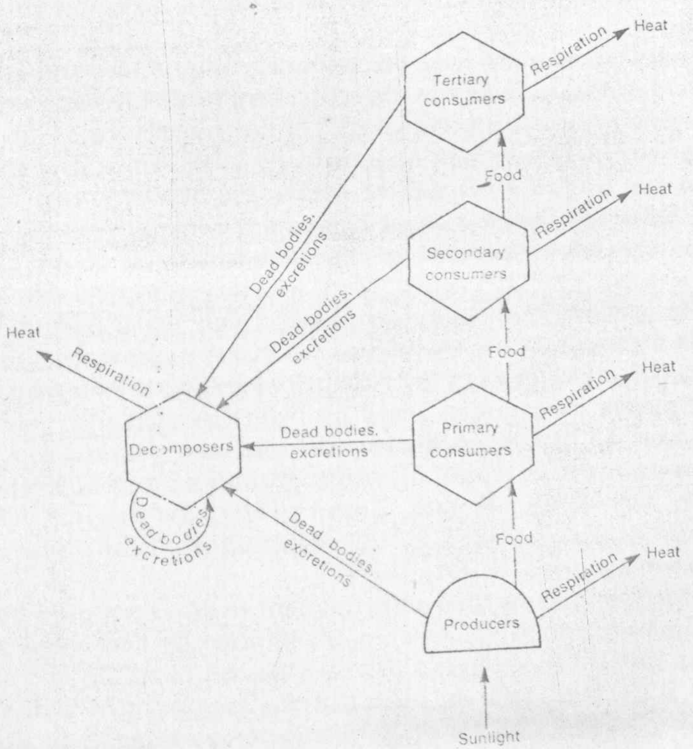

Figure 4–4. Energy flow in an ecosystem.

new individuals), but much is used for repair of tissues, moving around, and other activities that herbivores must perform to maintain themselves. Like the respiratory energy of plants, this energy is eventually converted to heat. Note that the herbivores have much less energy available to them than the plants originally produced in photosynthesis. The energy that the plants used in respiration is gone; also, some parts of the plant die before being eaten by herbivores and become food for decomposers, rather than for herbivores such as grasshoppers or deer. A good part of a plant leaf or the rest of a plant body is indigestible to most herbivores. These indigestible remains still contain energy and, by forming the major part of the feces of herbivores, become food for other decomposers.

The carnivores, or secondary consumers, obtain their energy from the herbivores in the same way that herbivores obtain theirs from plants. The carnivore uses some of the digested herbivore tissue for new cells, tissue, and producing young; the rest is respired to provide the energy for carrying on these activities. The energy available to the carnivore is, of course, much less than that taken in by the herbivore. Energy in materials that proved indigestible to the herbivore is gone and so is the large amount of energy used by the herbivores in their own maintenance. Also, like the primary consumer, the secondary consumer is not completely efficient in harvesting the available food nor in digesting what it does harvest.

Tertiary consumers feed on secondary consumers and quaternary consumers, if there are any in the ecosystem, feed on tertiary consumers. The foregoing processes occur at each of these levels (Fig. 4–5).

It is worthwhile to look quantitatively at the amount of energy lost between one trophic level and the next in the flow of energy in the ecosystem. Let us say that an average figure for the energy in sunlight striking one square meter of ground in the United States is about 1.5 million kilocalories per year (the actual figure will vary a bit depending on such factors as latitude and cloudiness). Only a very small fraction of this is stored in photosynthesis; we can use 1% as a very generous figure. Thus, about 15,000 kilocalories of the sunlight's energy are stored by plants in photosynthesis. The portion used by plants in their own maintenance may be from 15 to 75% of this amount, depending on the ecosystem. If 40% is considered as typical for plant respiration, then 60% of 15,000 is stored in new plant biomass. Consequently, the original 1.5 million kilocalories is now reduced to 9000 kilocalories potentially available to primary consumers.

In most ecosystems the energy in plant tissue is not used by grazers or browsers with high efficiency. Consumption by herbivores seems to vary over a wide range but is almost always less than 50% and is usually less than 20%. The rest of the plant material dies and goes to decomposer food chains. If we take 20% as another generous value, then about 1800 kilocalories of plant material are eaten by herbivores, or primary consumers. Of this amount, very roughly 10% is stored as new herbivore

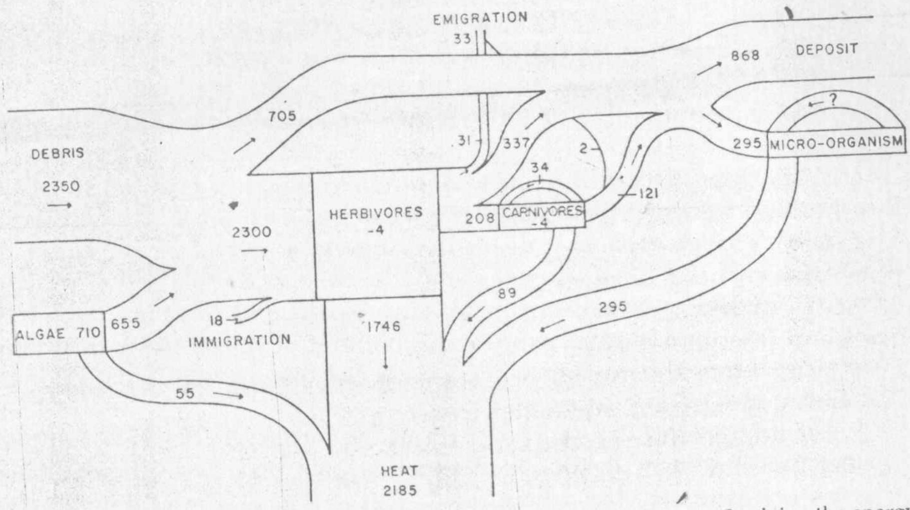

Figure 4–5. Energy flow for Root Spring, Concord, Massachusetts. Studying the energy flow through all the components of an ecosystem is an enormous task, and therefore most attempts involve many approximations. Many of the problems with precision were avoided in this study by dealing with a small, cold-water spring only 2 meters in diameter. The figures are kilocalories per square meter per year (figures in the herbivore and carnivore boxes are changes in standing crop). This ecosystem differs from the general example in the text in that import of energy in the form of organic matter, mainly leaves from surrounding trees, plays a large role. Not all of the energy entering is used, so that some goes into deposits on the bottom of the stream which will, in time, cause the spring to fill in (From J. M. Teal, "Community metabolism in a temperate cold spring," *Ecological Monographs*, 27(3):298, 1957. Copyright 1957 by the Ecological Society of America.)

tissue and is thus available to the secondary consumers, the first order carnivores. The other 90% is either used in maintenance of the herbivores and lost as heat or goes to decomposers as feces and excretions. Accordingly, about 180 of the 1800 kilocalories of plant material eaten by herbivores become new biomass.

If we assume that secondary consumers are slightly more efficient at harvesting the new biomass available to them, taking 30% instead of 20%, then 54 of the 180 kilocalories available in herbivores are ingested by first level carnivores. Using the same 10% efficiency figure that we used for the primary consumers for converting food to new biomass, these 54 kilocalories diminish to 5.4, which are stored as new carnivore protoplasm (Fig. 4–6). This amount is the energy potentially available to tertiary consumers. If we assume that they catch 30% and convert 10% of that, as we did for secondary consumers, then they ingest food containing 1.6 kilocalories and are able to produce new biomass containing 0.16 kilocalorie.

From this it should be plain why the pyramids of number and biomass occur. Less and less energy is available at each level. If a herbivore can find as much food as it needs in one acre, a secondary consumer of the same size will need ten acres and a tertiary consumer will need 100. This is one main reason, of course, why hawks and trout are relatively rare and mice and bluegill sunfish are common. It is also the reason why two people in a square mile of wilderness can live on trout but 2000 men in one square mile must eat rice.

Let us consider one more fact about decomposers. We have lumped under this one term all the organisms that gain their energy from dead bodies and excreta, but complicated food webs also exist among this group of organisms. Very small insects and other invertebrates may feed upon dead leaves that have fallen to the ground; these animals may in turn be eaten by small carnivorous invertebrates. Bacteria and fungi may grow on the remains of fallen leaves and the bacteria and fungi may be eaten by other invertebrates. The portion of the ecosystem which starts with dead protoplasm and is located mainly in the soil or in the bottom mud of bodies of water has not yet been well studied, but in many ecosystems, possibly most, the total amount of energy that flows in this way is greater than that which travels the more conspicuous route, from live plant to grazer to conspicuous carnivore (Fig. 4–7).

BIOMASS

In the previous section we discussed energy *flow*. At any one time each trophic level contains some amount of energy stored as biomass, often referred to as the *standing crop*. The pyramid of biomass gives an indication of the amount of energy present at a particular time. To understand the relationship between energy flow and the energy present as

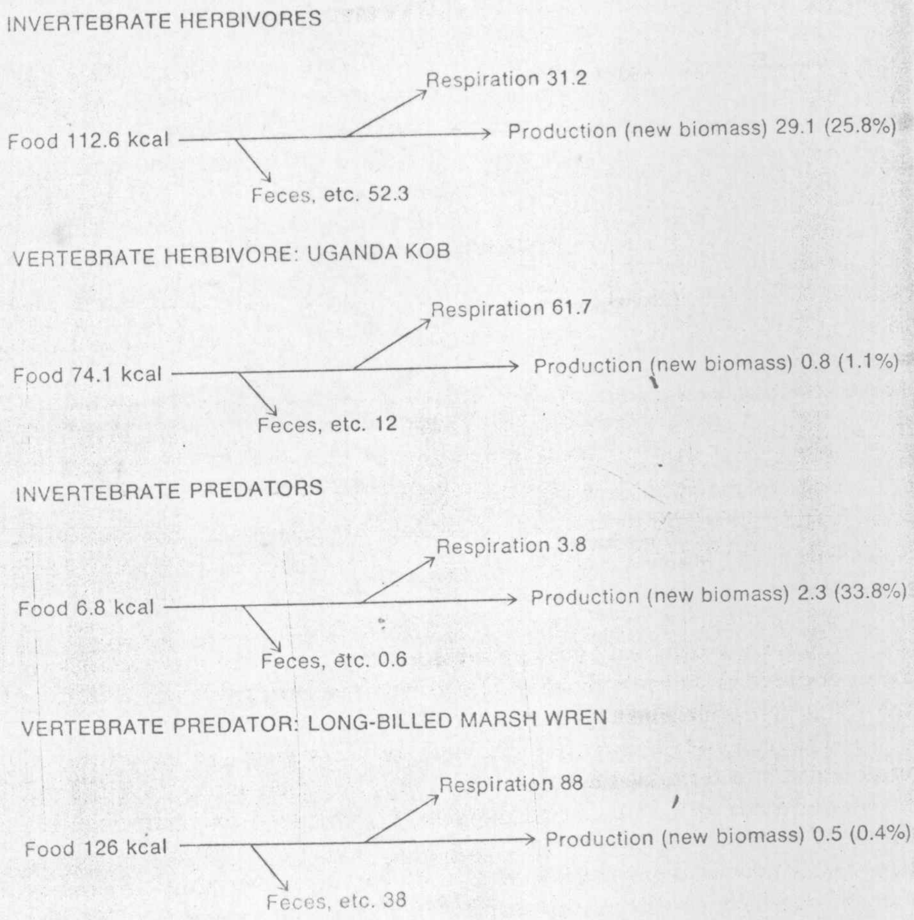

Figure 4–6. We used 10% as an average for the efficiency with which consumers convert food into new protoplasm but the actual figures vary widely. One generalization that helps to make sense out of the variations is that homoiotherms are generally less efficient than poikilotherms. One reason is the substantial amount of energy homoiotherms must use just to maintain their body temperature. The diagram above compares energy flow through the invertebrate herbivores and predators (all poikilotherms) of a Tennessee grassland with energy flow through two populations of homoiotherms, an antelope in Africa and an insectivorous bird in a Georgia salt marsh. The figures are kilocalories per square meter per year, and the efficiency of conversion of foods to biomass is given in parentheses. Efficiencies vary from less than 1 to more than 30%, with the vertebrates (homoiotherms) being the low ones. (Data on: invertebrate herbivores and invertebrate predators from R. I. Van Hook, "Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem," *Ecological Monographs*, 41:20, 1971; vertebrate herbivore from H. K. Buechner and F. B. Golley, "Preliminary estimation of energy flow in Uganda kob," in K. Petrusewicz, ed., *Secondary Productivity of Terrestrial Ecosystems*, Polish Academy of Science, 1967, p. 252; vertebrate predator from H. W. Kale, "Ecology and bioenergetics of the long-billed marsh wren *Telmatodytes palustria griseus* (Brewster) in Georgia salt marshes," Nuttall Ornithological Club, Publication No. 5, 1965, p. 142.)

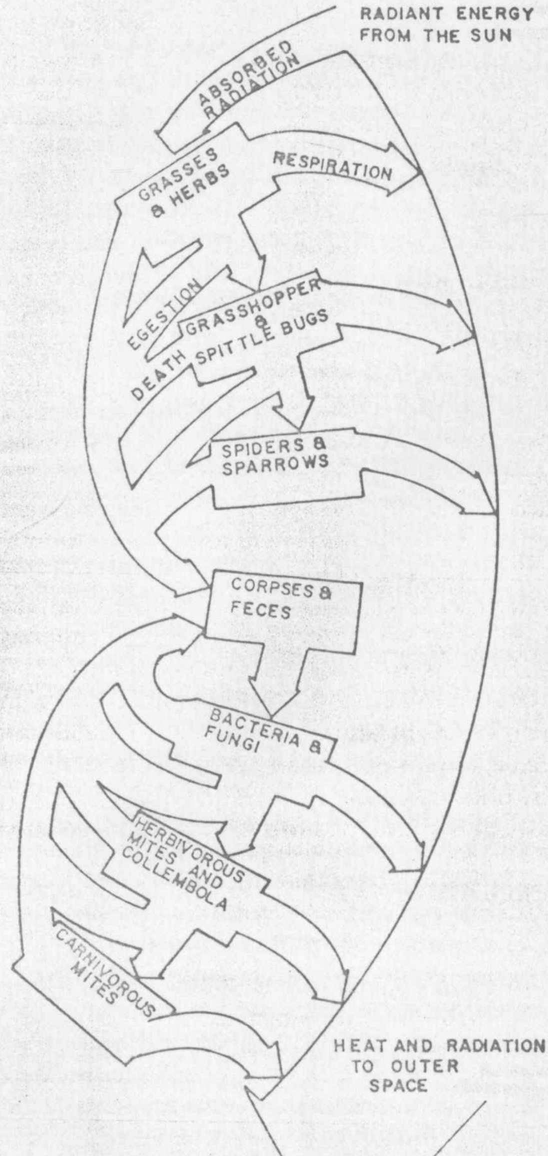

Figure 4–7. The importance of food chains that start with dead leaves, limbs, carrion, and "corpses and feces" in general is emphasized in this diagram of energy flow in an old field in Michigan. The food chains involving grasshoppers and sparrows are what we see when we look at a grassland but the food chains of bacteria and mites often process a greater proportion of the energy that the green plants have fixed. (From M. D. Engelmann, "The role of soil arthropods in the energetics of an old field community," *Ecological Monographs,* 31:235, 1961. Copyright 1961 by the Ecological Society of America.)

standing crop we can compare energy flow with cash flow in and out of your checking account. Suppose that your account has has $9.41 in it at the beginning of the year, and during the course of the year you put money in and take money out. If $500.00 is deposited and $500.00 taken out, then $9.41 still remains at the end of the year. The $9.41 is analogous to standing crop and the cash flow of $500.00 corresponds to energy flow.

Energy is deposited in an ecosystem through photosynthesis and withdrawn as respiratory energy at the various trophic levels. If as much energy goes in as comes out during a year, then the ecosystem is at an energetic *steady state*. If photosynthesis is greater than respiration in all the trophic levels combined (corresponding to putting $500.00 in the account and only taking out $400.00), energy must be accumulating somewhere in the system—either as larger organisms (for example, in tree growth), more organisms, or through storage in litter and humus. An ecosystem may also be on the negative side of a steady state; in a given year less energy may enter the system than is lost from it, in which case there is a net loss of energy from the system. The positive energy balance situation is probably common in early stages of community development (Chap. 5). The situation of negative energy balance probably cannot last for very many years but occurs under certain conditions such as severe drought. In a very dry year in a grassland much of the litter which has accumulated in preceding years may be decomposed and the year's production may be too small to make up the loss.

Table 4–1 compares energy flow in an immature forest (a pine plantation in England) and a mature one (a rain forest in Puerto Rico). The rain forest is obviously much more productive but the object of the comparison is to show that the rain forest is at an energetic steady state whereas the pine plantation is not. In the rain forest the sum of the energy used in respiration by the plants, animals, and bacteria equals the energy fixed in photosynthesis. In the pine plantation there is more energy fixed in photosynthesis than is used. The excess is ***net community production*** which accumulates in the form of wood in tree trunks, litter, etc.

PRODUCTIVITY

The total energy storage by autotrophs in an ecosystem is referred to as *gross production*. The plants themselves use a considerable amount of

Table 4–1 ENERGY FLOW IN TWO FORESTS*

	Immature Forest ($Kcal/m^2/year$)	Mature Forest ($Kcal/m^2/year$)
Total photosynthesis (gross primary production, GPP)	12,200	45,000
Plant respiration	4,700	32,000
New plant tissue (net primary production, NPP)	7,500	13,000
Heterotrophic respiration†	4,600	13,000
Net community production (NCP)	2,900	Little or none
Ratio NCP/GPP	23.8%	0%

*Modified from Odum, E. P., *Fundamentals of Ecology*, Philadelphia, W. B. Saunders, 1971, Table 3–5, p. 46.

†Includes herbivores, carnivores, bacteria, and other decomposers.

this in their own respiration. The amount of stored energy left after the plants' respiration is ***net production***.* A year is a convenient interval to use in stating productivity, but daily or growing season production may also be studied. Energy units and weight are two different ways of expressing productivity. Either may be used because the energy is stored in the organic compounds which compose plant bodies. Dry weights are taken because the water content of different kinds of organisms varies.

The energy content of a given weight of plant or animal material is calculated by burning the dry material in a calorimeter and determining the amount of heat given off. This has been done for various kinds of plant and animal materials. The amount of heat given off by plant material runs about 4-4½ kilocalories per gram of oven-dried plant matter; animal material is usually 5-5½ kilocalories per gram of dry weight. Using these figures (which will be only approximate for a particular type of plant or animal) we can convert from weight to energy and vice versa.

Annual net production is a convenient basis for comparing various ecosystems because it is the energy potentially available to the organisms of the trophic levels past the producers for the year. Net yearly production ranges from zero in the driest deserts and other habitats too extreme to support plants to greater than 5000 grams per square meter (Table 4–2). This latter value, upwards of 11 pounds of plant material added to one square meter in one year, is a sizable amount of growth. Annual net production is probably between 500 and 2000 grams per square meter over much of the temperate part of the earth. On a pounds per acre basis, a familiar way of expressing agricultural production in English-speaking countries, this is about 5,000 to 18,000 pounds per acre. These are not actually *yields* in the agricultural sense since they include all new protoplasm including stems, bark, roots, and pollen. Humans could obtain this amount of plant material as food only if they were able to eat all parts of the plant and even then only if they were able and willing to eliminate all other animals that might also consume parts of the plants.

What environmental factors contribute to high annual productivity? A good moisture supply, a long growing season, warm temperatures, and high fertility are all favorable. It is not surprising that marshes and estuaries where moisture is abundant and nutrients are supplied by runoff from the land have a high rate of production. Nor is it surprising that tropical ecosystems with a long growing season and high temperatures have a high annual production and that deserts with their low rainfall and high evaporation rate are unproductive. However, it is interesting to note that the productivity of the open ocean is scarcely more than that of deserts. The main reason appears to be a scarcity of chemical nutrients—phosphates, nitrates, or possibly iron. The only really productive

*Sometimes these are called gross and net *primary* production, with energy storage at consumer levels of the ecosystem then referred to as *secondary* production.