The Energy Cycle of the Biosphere

Life is maintained by the finite amount of solar energy that is fixed by green plants. An increasing fraction of that energy is being diverted to the direct support of one living species: man

by George M. Woodwell

The energy that sustains all living systems is solar energy, fixed in photosynthesis and held briefly in the biosphere before it is reradiated into space as heat. It is solar energy that moves the rabbit, the deer, the whale, the boy on the bicycle outside my window, my pencil as I write these words. The total amount of solar energy fixed on the earth sets one limit on the total amount of life; the patterns of flow of this energy through the earth's ecosystems set additional limits on the kinds of life on the earth. Expanding human activities are requiring a larger fraction of the total and are paradoxically making large segments of it less useful in support of man.

Solar energy has been fixed in one form or another on the earth throughout much of the earth's 4.5-billion-year history. The modern biosphere probably had its beginning about two billion years ago with the evolution of marine organisms that not only could fix solar energy in organic compounds but also did it by splitting the water molecule and releasing free oxygen.

The beginning was slow. Molecular oxygen released by marine plant cells accumulated for hundreds of millions of years, gradually building an atmosphere that screened out the most destructive of the sun's rays and opened the land to exploitation by living systems [see "The Oxygen Cycle," by Preston Cloud and Aharon Gibor, page 110]. The colonization of the land began perhaps 400 million years ago. New species evolved that derived more energy from a more efficient respiration in air, accelerating the trend.

Evolution fitted the new species together in ways that not only conserved energy and the mineral nutrients utilized in life processes but also conserved the nutrients by recycling them, releasing more oxygen and making possible the fixation of more energy and the support of still more life. Gradually each landscape developed a flora and fauna particularly adapted to that place. These new arrays of plants and animals used solar energy, mineral nutrients, water and the resources of other living things to stabilize the environment, building the biosphere we know today.

The actual amount of solar energy diverted into living systems is small in relation to the earth's total energy budget [see "The Energy Cycle of the Earth," by Abraham H. Oort, page 54]. Only about a tenth of 1 percent of the energy received from the sun by the earth is fixed in photosynthesis. This fraction, small as it is, may be represented locally by the manufacture of several thousand grams of dry organic matter per square meter per year. Worldwide it is equivalent to the annual production of between 150 and 200 billion tons of dry organic matter and includes both food for man and the energy that runs the life-support systems of the biosphere, namely the earth's major ecosystems: the forests, grasslands, oceans, marshes, estuaries, lakes, rivers, tundras and deserts.

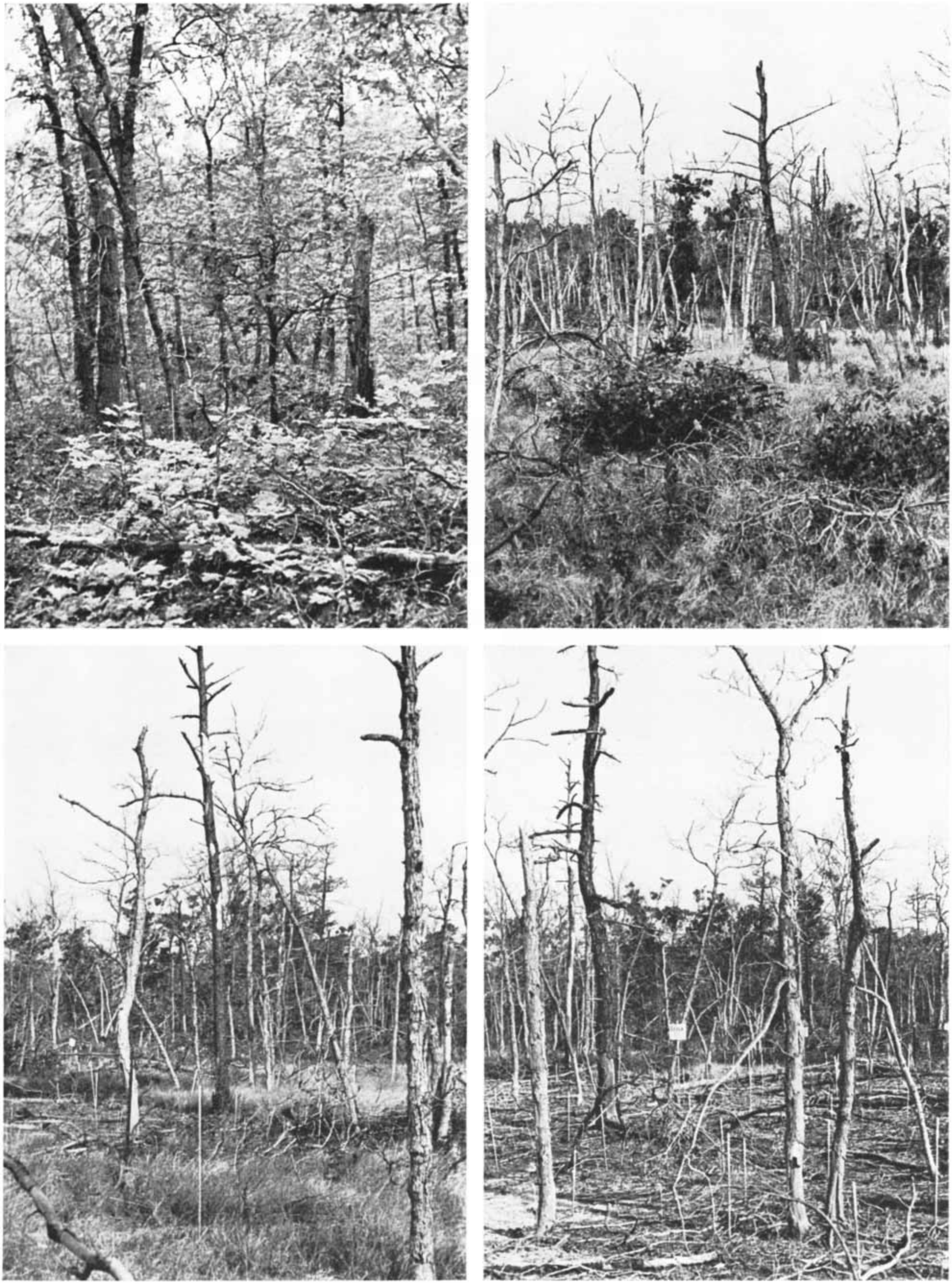
The complexity of ecosystems is so great as to preclude any simple, single-factor analysis that is both accurate and satisfying. Because of the central role of energy in life, however, an examination of the fixation of energy and its flow through ecosystems yields understanding of the ecosystems themselves. It also reveals starkly some of the obscure but vital details of the crisis of environment.

More than half of the energy fixed in photosynthesis is used immediately in the plant's own respiration. Some of it is stored. In land plants it may be transferred from tissues where it is fixed, such as leaves, to other tissues where it is used immediately or stored. At any point it may enter consumer food chains.

There are two kinds of chain: the grazing, or browsing, food chains and the food chains of decay. Energy may be stored for considerable periods in both kinds of chain, building animal populations in the one case and accumulations of undecomposed dead organic matter and populations of decay organisms in the other. The fraction of the total energy fixed that flows into each of these chains is of considerable importance to the biosphere and to man. The worldwide increase in human numbers not only is shifting the distribution of energy within ecosystems but also requires that a growing fraction of the total energy fixed be diverted to the direct support of man. The implications of such diversions are still far from clear.

Before examining the fixation and flow of energy in ecosystems it is important to consider the broad pattern of their development throughout evolution. If one were to ascribe a single objective to evolution, it would be the perpetuation of life. The entire strategy of evolution is focused on that single end. In realizing it evolution divides the resources of any

GREEN PLANTS are the "primary producers" of the biosphere, converting solar energy into organic compounds that maintain the plants and other living things. Forests, which cover about a tenth of the earth's surface, fix almost half of the biosphere's total energy. The photograph on the opposite page, which was made in the Mazumbai forest in Tanzania, illustrates the rich diversity typical of a relatively mature ecosystem, with many species arranged in a structure that apportions the available solar energy as effectively as possible.

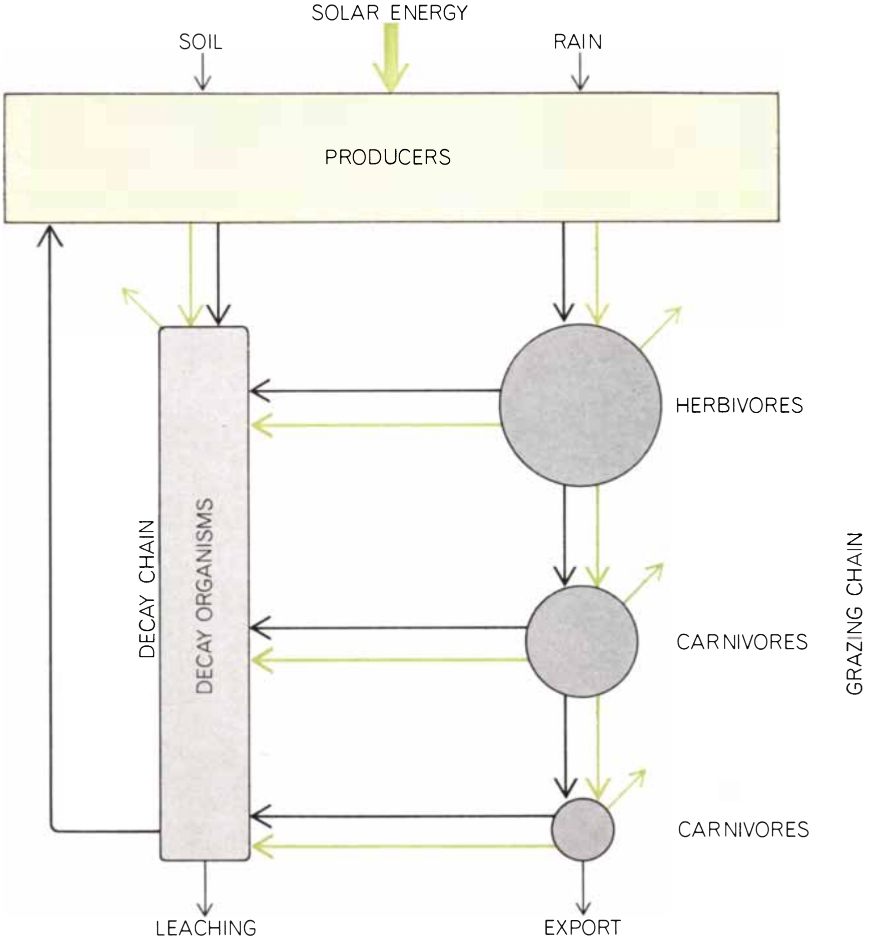


STRUCTURE OF FORESTS changes with disturbance according to well-defined patterns. The photographs show the loss of structure in an oak-pine forest at the Brookhaven National Laboratory as a result of continued exposure to gamma radiation. Exposure of the intact forest (*top left*) to radiation first destroys pine trees and then other trees, leaving tree sprouts, shrubs and ground cover (*top right*). Longer exposure kills shrubs (*bottom left*) and finally the sedge, grasses and herbs of the ground cover (*bottom right*).

location, including its input of energy, among an ever increasing number of different kinds of users, which we recognize as plant and animal species.

The arrangement of these species in today's ecosystems is a comparatively recent event, and the ecosystems continue to be developed by migration and continuing evolution. Changes accrue slowly through a conjoint evolution that is not only biological but also chemical and physical. The entire process appears to be open-ended, continuous, self-augmenting and endlessly versatile. It builds on itself, not merely preserving life but increasing the capacity of a site to support life. In so doing it stabilizes the site and the biota. Mineral nutrients are no longer leached rapidly into watercourses; they are conserved and recirculated, offering opportunities for more evolution. Interactions among ecosystems are exploited and stabilized, by living systems adapted to the purpose. The return of the salmon and other fishes from years at sea to the upper reaches of rivers is one example; impoverished upland streams are thus fertilized with nutrients harvested in the ocean, opening further possibilities for life.

The time scale for most of these developments, particularly in the later stages when many of the species have large bodies and long life cycles, is very long. Such systems are for all practical purposes stable. These are the living systems that have shaped the biosphere. They are self-regulating and remarkably resilient. Now human activities have become so pervasive as to affect these systems all over the world. What kinds of change can we expect? The answers depend on an understanding of the patterns of evolution and on a knowledge of the structure and function of ecosystems. And the fixation and flow of energy is at the core.



NET FLOW OF ENERGY (*colored arrows*) **and nutrients** (*black arrows*) **through a natural community is diagrammed in simplified form. In a mature community all the energy fixed by the primary producers, the plants, is dissipated as heat in the respiration of the plants, the consumers (herbivores and successive echelons of carnivores) and decay organisms. Almost all nutrients are eventually recycled, however, to renew plant and animal populations.**

Much of our current understanding of ecosystems has been based on a paper published in *Ecology* in 1942 by Raymond L. Lindeman, a young colleague of G. Evelyn Hutchinson's at Yale University. (It was Lindeman's sixth and last paper; his death at the age of 26 deprived ecology of one of its most outstanding intellects.) Lindeman drew on work by earlier scholars, particularly Arthur G. Tansley and Charles S. Elton of England and Frederick E. Clements and Victor E. Shelford of the U.S., to examine what he called the "trophic-dynamic aspect" of ecology. He called attention to the fixation of energy by natural ecosystems and to the quantitative relations that must exist in nature between the different users of this energy as it is divided progressively among the various populations of an ecosystem.

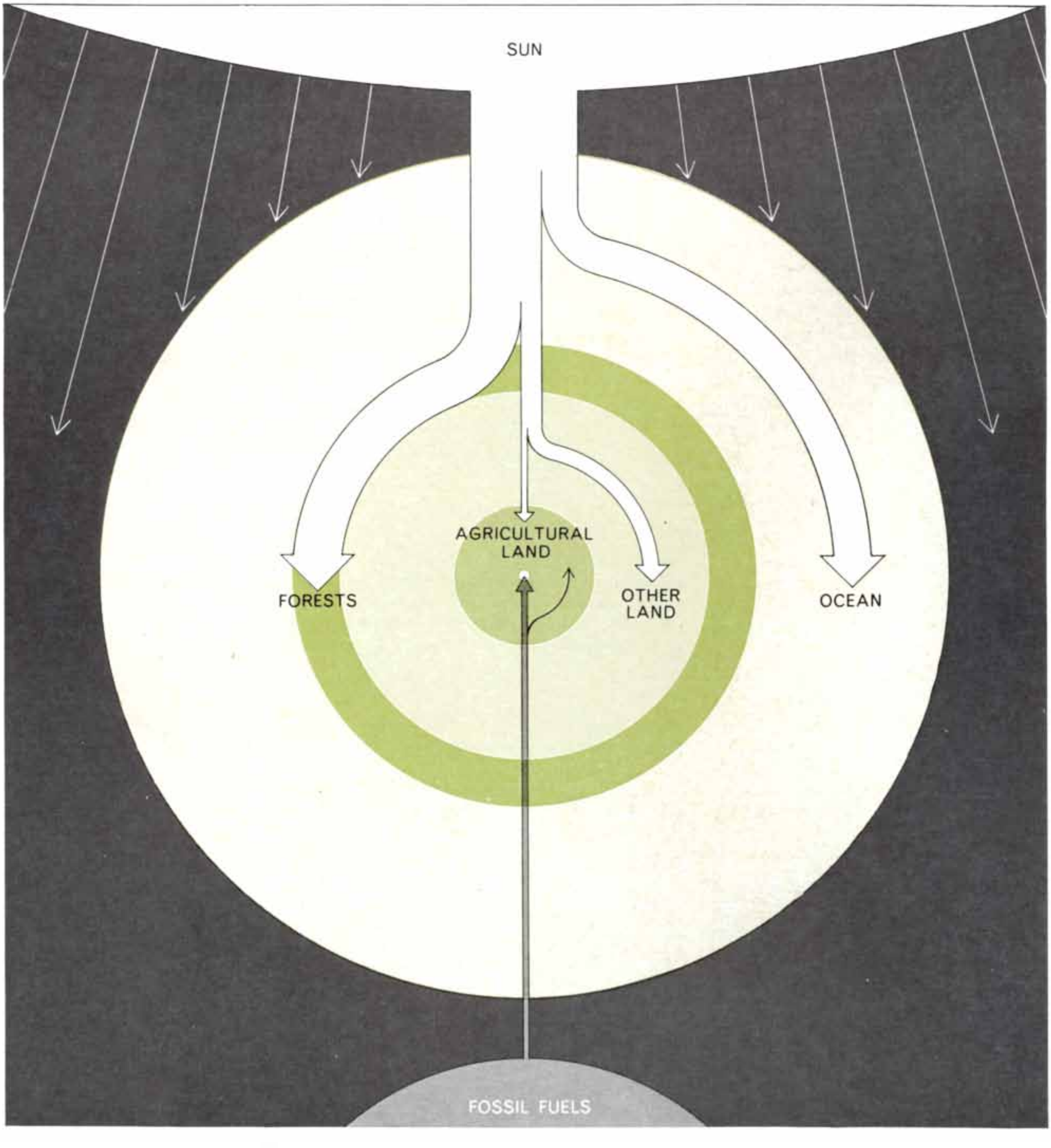
Lindeman's suggestions were provocative. They stimulated a series of field and laboratory studies, all of which strengthened his synthesis. One of the most useful generalizations of his approach, sometimes called "the 10 percent law," simply states that in nature some fraction of the energy entering any population is available for transfer to the populations that feed on it without serious disruption of either. The actual amount of energy transferred probably varies widely. It seems fair to assume that in the grazing chain perhaps 10 to 20 percent of the energy fixed by the plant community can be transferred to herbivores, 10 to 20 percent of the energy entering the herbivore community can be transferred to the first level of carnivores and so on. In this way what is called a mature community may support three or four levels of animal populations, each related to its food supply quantitatively on the basis of energy fixation.

No less important than the grazing food chains are the food chains of decay. On land these chains start with dead organic matter: leaves, bits of bark and branches. In water they originate in the remains of algae, fecal matter and other organic debris. The organic debris may be totally consumed by the bacteria, fungi and small animals of decay, releasing carbon dioxide, water and heat. It may enter far more complex food webs, potentially involving larger animals such as mullet, carp, crabs and ultimately higher carnivores, so that although it is convenient to think of the grazing and decay routes as being distinct, they usually overlap.

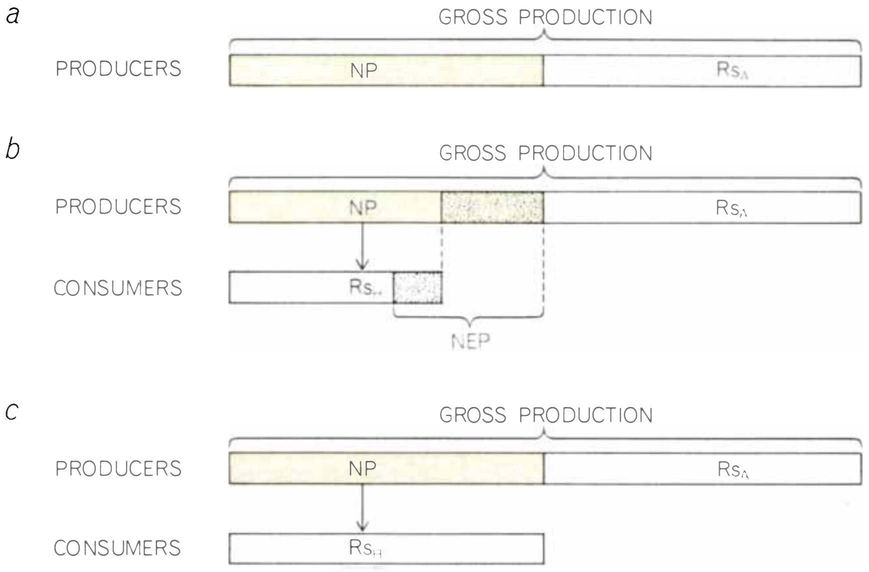
The decay food chain does not always function efficiently. Under certain circumstances it exhausts all the available oxygen. Decay is then incomplete; its products include methane, alcohols, amines, hydrogen sulfide and partially decomposed organic matter. Its connections to the grazing food chain are reduced or broken, with profound effects on living systems. Such shifts are occurring more frequently in an increasingly man-dominated world.

How much energy is fixed by the major ecosystems of the biosphere? The question is more demanding than it may appear because measuring energy fixation in such diverse vegetations as forests, fields and the oceans is most difficult. Rates of energy fixation vary from day to day—even from minute to minute—and from place to place. They are affected by many factors, including light and the concentration of carbon dioxide, water and nutrients.

In spite of the difficulties in obtaining unequivocal answers several attempts have been made to appraise the total amounts of energy fixed by the earth's ecosystems. Most recently Robert H.



ENERGY FIXED by the earth's primary producers is equivalent to about 164 billion metric tons of dry organic matter a year, according to Robert H. Whittaker and Gene E. Likens of Cornell University. About 5 percent of the energy is fixed by agricultural ecosystems and is utilized directly by man, one species among millions. Man also draws annually on fossil fuel reserves for about the same amount of energy. In this anthropocentric view of the biosphere the area of the concentric rings is proportional to the major ecosystems' share of the surface area of the earth (indicated in millions of square kilometers). The width of the arrows is proportional to the amount of energy fixed in each ecosystem and contributed by fossil fuels (indicated in billions of metric tons of dry matter per year). The intensity of the color in each ring suggests the productivity (production per unit area) of each ecosystem.



ENERGY IS UTILIZED by producers and consumers as shown here. In the case of a single green plant (*a*) some of the total energy fixed, or gross production, is expended in the plant's own respiration (Rs_A) and the rest goes into net production (NP), or new tissue. In a successional plant-and-animal community (*b*) some of the net production is stored as growth, contributing to net ecosystem production (NEP); the rest is used by consumers, which expend most of it in respiration (Rs_H) and store some as growth, adding to net ecosystem production. In a mature community (*c*) all the energy fixed is used in respiration.

Whittaker and Gene E. Likens of Cornell University have estimated that in all the earth's ecosystems, both terrestrial and marine, 164 billion metric tons of dry organic matter is produced annually, about a third of it in the oceans and two-thirds of it on land. This "net production" represents the excess of organic production over what is required to maintain the plants that fixed the energy; it is the energy potentially available for consumers.

Virtually all the net production of the earth is consumed annually in the respiration of organisms other than green plants, releasing carbon dioxide, water and the heat that is reradiated into space. The consumers are animals, including man, and the organisms of decay. The energy that is not consumed is either stored in the tissues of living organisms or in humus and organic sediments.

The relations between the producers and the consumers are clarified by two simple formulas. Consider the growth of a single green plant, an "autotroph" that is capable of fixing its own solar energy. Some of the energy it fixes is stored in organic matter that accumulates as new tissue. The amount of the new tissue, measured as dry weight, is the net production. This does not, however, represent all the energy fixed. Some energy is required just to support the living tissues of the plant. This is energy used in respiration.

The total energy fixed, then, is partitioned immediately within the plant according to the equation $GP - Rs_A = NP$. The total amount of energy fixed is gross production (GP); Rs_A is the energy used in the respiration of the autotrophic plant, and the amount of energy left over is net production (NP). The growth of a plant is measurable as net production, which can be expressed in any of several different ways, including energy stored and dry weight.

The same relations hold for an entire plant community and for the biosphere as a whole. If we consider not only the plants but also the consumers of plants and the entire food web, including the organisms of decay, we must add a new unit of respiration without adding any further producers. That is what happens as an ecosystem matures: consumer populations increase substantially, adding to the respiration of the plants the respiration (Rs_H) of the heterotrophs, the organisms that obtain their energy from the photosynthesizing plants. For an ecosystem (the total biota of any unit of the earth's surface) NEP equals $GP - (Rs_A + Rs_H)$. NEP is the net ecosystem production, the net increase in energy stored within the system. $Rs_A + Rs_H$ is the total respiration of the ecosystem.

This last equation establishes the important distinction between a "successional," or developmental, ecosystem and a "climax," or mature, one. In the successional system the total respiration is less than the gross production, leaving energy (NEP) that is built into structure and adds to the resources of the site. (A forest of large trees obviously has more space in it, more organic matter and probably a wider variety of microhabitats than a forest of small trees.) In a climax system, on the other hand, all the energy fixed is used in the combined respiration of the plants and the heterotrophs. NEP goes to zero: there is no energy left over and no net annual storage. Climax ecosystems probably represent a most efficient way of using the resources of a site to sustain life with minimum impact on other ecosystems. It is of course such ecosystems that have dominated the biosphere throughout recent millenniums.

These general relations are clarified if one asks, with regard to a specific ecosystem, how much energy is fixed and how it is used, and how efficient the ecosystem is in harvesting solar energy and supporting life. The answers are found by solving the simple production equations, but in order to solve them one must measure the metabolism of an entire unit of landscape. Such studies are being attempted in many types of ecosystem under the aegis of the International Biological Program, a major research effort designed to examine the productivity of the biosphere. The example I shall give is drawn from research in an oak-pine forest at the Brookhaven National Laboratory.

The research has spanned most of a decade and has involved many contributors. A most important contribution was made by Whittaker, who collaborated with me in completing a detailed description of the structure of the forest, including the total amount of organic matter, the weight and area of leaves, the weight of roots and the amount of net production. The techniques developed in that work are now being used in many similar studies. Such data are necessary to relate other measurements, including measurements of the gas exchange between leaves and the atmosphere, to the entire forest and so provide an additional measurement of net production and respiration.

A major problem was measuring the forest's total respiration. We used two techniques. First, Winston R. Dykeman and I took advantage of the frequent inversions of temperature that occur in central Long Island and used the rate of accumulation of carbon dioxide during these inversions as a direct measurement of total respiration. The inversions are nocturnal; this eliminates the effect of photosynthesis, which of course proceeds only in daylight.

During an inversion the temperature of the air near the ground is (contrary to the usual daytime situation) lower than that of the air at higher elevations. Since the cooler air is denser, the air column remains vertically stable for as much as several hours; the carbon dioxide released by respiration accumulates, and its buildup at a given height is an index of the rate of respiration at that height. The calculation of the buildup during more than 40 inversions in the course of a year provided one measure of total respiration [*see top illustration on page 72*]. A second measurement came from a detailed study of the rates of respiration of various segments of the forest (including the branches and stems of trees) and the soil.

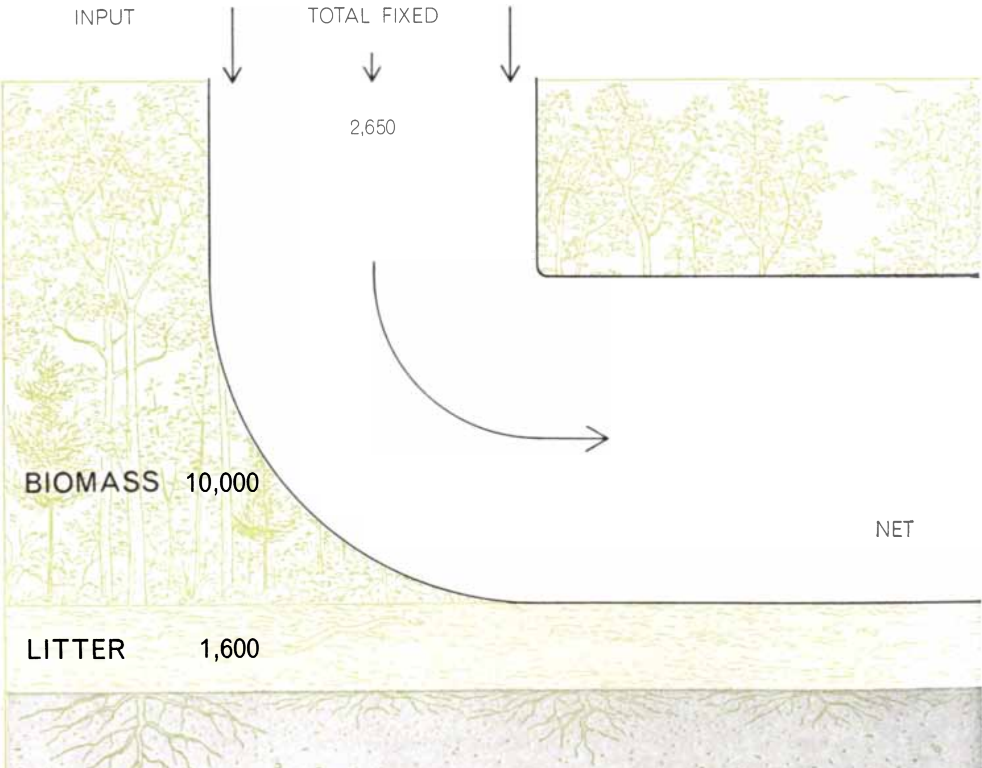
The estimates available from these studies and others are converging on the following solution of the production equations, all in terms of grams of dry organic matter per square meter per year: The gross production is 2,650 grams; the net production, 1,200 grams; the net ecosystem production, or net storage, 550 grams, and the total respiration, or energy loss, 2,100 grams, of which Rs_A is 1,450 and Rs_H is 650 [*see illustration on these two pages*]. The forest is obviously immature in the sense that it is still storing energy (NEP) in an increased plant population. The ratio of total respiration to gross production (2,100/2,650) suggests that the forest is at about 80 percent of climax and confirms other studies that show that the forest is "late successional."

The net production of the Brookhaven forest of 1,200 grams per square meter per year is in the low middle range for forests and is typical of the productivity of small-statured forests. The efficiency of this forest in using the annual input of solar energy effective in photosynthesis is about .9 percent. Large-statured forests (moist forests of the Temperate Zone, where nutrients are abundant, and certain tropical rain forests) have a net productivity ranging up to several thousand grams per square meter per year. They may have an efficiency approaching 3 percent of the usable energy available throughout the year at the surface of the ground, but usually not much more.

Sugarcane productivity in the Tropics has been reported as exceeding 9,000 grams per square meter per year. The new strains of rice that are contributing to the "green revolution" have a maximum yield under intensive triple-cropping regimes that may approach 2,000 grams of rice per square meter per year. Over large areas the yield is much lower, seldom exceeding 350 to 400 grams of milled rice per square meter per year. These yields are to be compared with corn yields in the U.S., which approach 500 grams. (The rice and corn yields are expressed as grain, not as total net production as we have been discussing it. Net production including the chaff, stems, leaves and roots is between three and five times the harvest of grain. Thus the net production of the most productive agriculture is 6,000 to 10,000 grams, probably the highest net production in the world. Most agriculture, however, has net production of 1,000 to 3,000 grams, the same range as most forests.)

The high productivities of agriculture are somewhat misleading in that they are bought with a contribution of energy from fossil fuels: energy that is applied to cultivate and harvest the crop, to manufacture and transport pesticides and fertilizers and to provide and control irrigation. The cost accounting is incomplete; these systems "leak" pesticides, fertilizers and often soil itself, injuring other ecosystems. It is clear, however, that the high yields of agriculture are dependent on a subsidy of energy that was fixed as fossil fuels in previous ages and is available now (and for some decades to come) to support large human populations. Without this subsidy or some other source of power, yields would drop. They may suffer in any case as it becomes increasingly necessary to reduce the interactions between agriculture and other ecosystems. One sign is the progressive restriction in the use of insecticides because of hazards far from where they are applied. Similar restraint may soon be necessary in the use of herbicides and fertilizers.

The oceans appear unproductive compared with terrestrial ecosystems. In separate detailed analyses of the fish production of the world's oceans William E. Ricker of the Fisheries Research Board of Canada and John H. Ryther of the Woods Hole Oceanographic Institution recently emphasized that the oceans are far from an unlimited resource. The net production of the open ocean is about



ENERGY RELATIONSHIPS were worked out for an oak-pine forest at the Brookhaven National Laboratory. Of the annual gross production of 2,650 grams of dry matter per

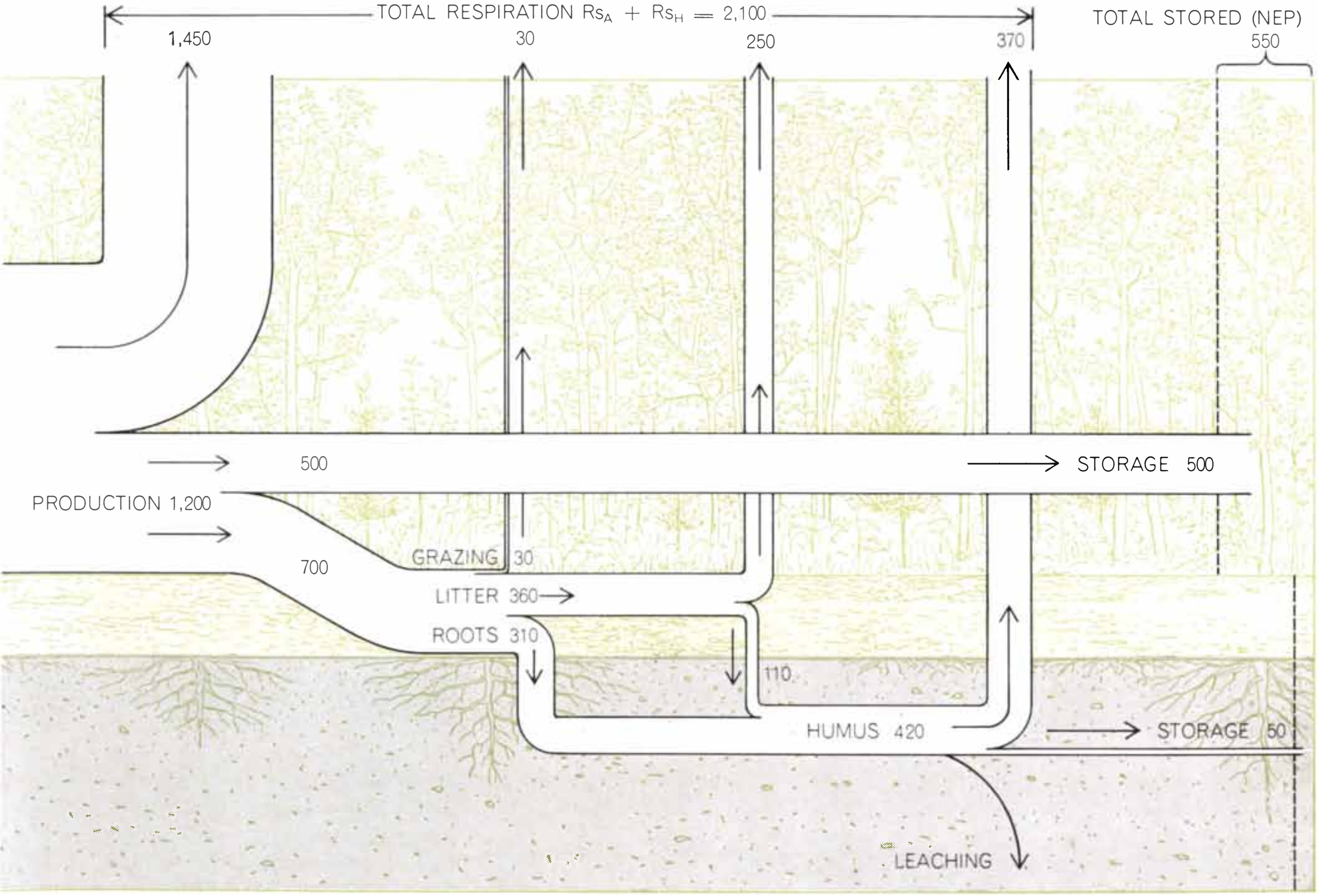
50 grams of fixed carbon per square meter per year. Areas of very high productivity, including coastal areas and areas of upwelling where nutrients are abundant, do not average more than 300 grams of carbon. The mean productivity of the oceans, according to this analysis, would be about 55 grams of carbon, equivalent to between 120 and 150 grams of dry organic matter.

Inasmuch as the highest productivity of enriched areas of the ocean barely approaches that of diminutive forests such as Brookhaven's, the oceans do not appear to represent a vast potential resource. On the contrary, Ryther suggests on the basis of an elaborate analysis of the complex trophic relations of the oceans that "it seems unlikely that the potential sustained yield of fish to man is appreciably greater than 100 million [metric] tons [wet weight]. The total world fish landings for 1967 were just over 60 million tons, and this figure has been increasing at an average rate of about 8 percent per year for the past 25 years.... At the present rate, the industry can expand for no more than a decade." Ricker comes to a similar conclusion. Neither he nor Ryther appraised the effects on the productivity of the oceans of the accumulation of toxic substances such as pesticides, of industrial and municipal wastes, of oil production on the continental shelves, of the current attempts at mining the sea bottom and of other exploitation of the seas that is inconsistent with continued harvesting of fish.

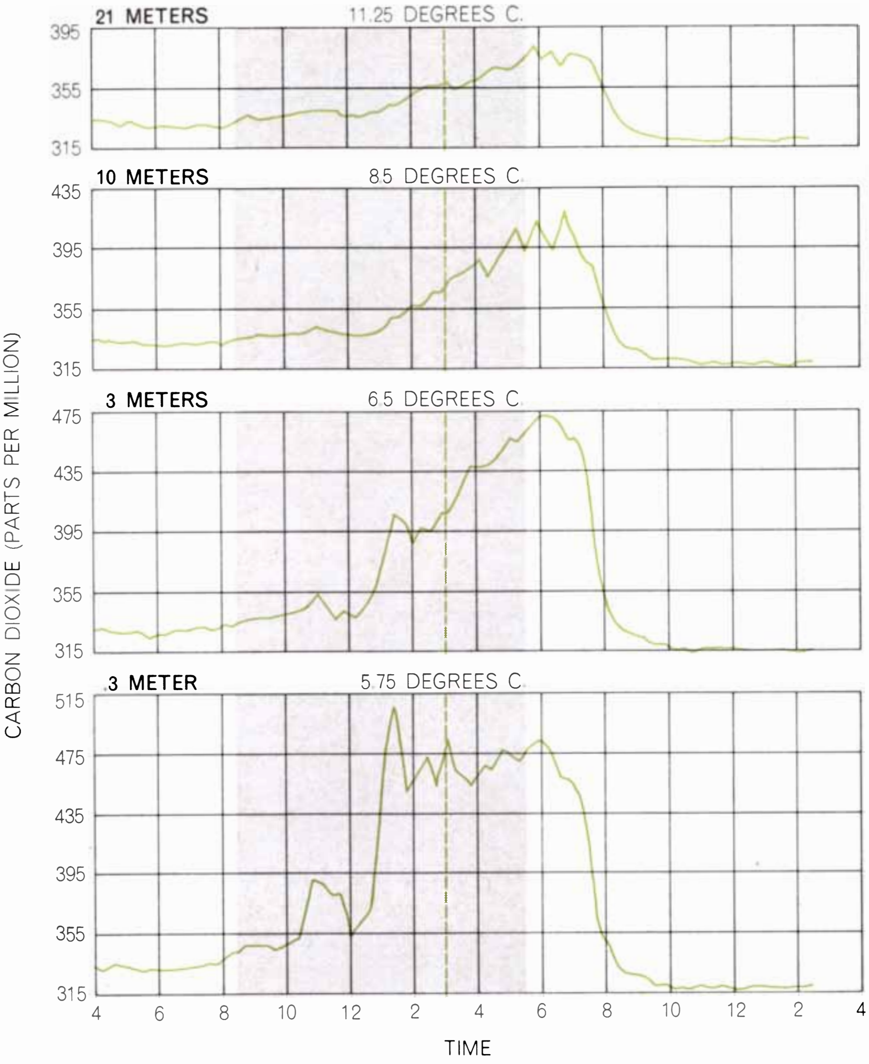
The available evidence suggests that, in spite of the much larger area of the oceans, by far the greater amount of energy is fixed on land. The oceans, even if their productivity can be preserved, do not represent a vast unexploited source of energy for support of larger human populations. They are currently being exploited at close to the maximum sustainable rate, and their continued use as a dump for wastes of all kinds makes it questionable whether that rate will be sustained.

A brief consideration of the utilization of the energy fixed in the Brookhaven forest will help to clarify this point. The energy fixed by this late-successional forest is first divided between net production and immediate use in plant respiration, with about 55 percent being used immediately. (The ratio of 55 percent going directly into respiration appears consistent for the Temperate Zone forests examined so far; the ratio appears to rise in the Tropics and to decline in higher latitudes.) The net production is divided among herbivores, decay and storage. In the Brookhaven forest herbivore populations have been reduced by the exclusion of deer, leaving as the principal herbivores insects and limited populations of small mammals.

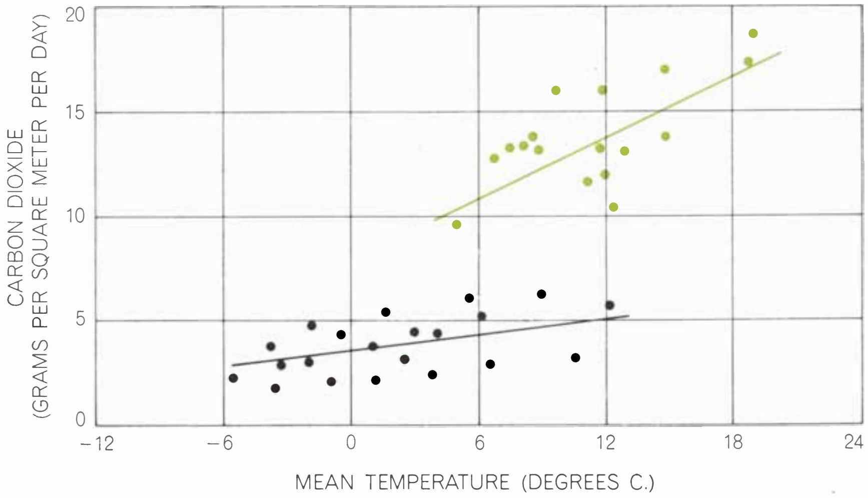
Our estimates indicate that only a few percent of the net production is consumed directly by herbivores (a low rate in comparison with other ecosystems). Practically all this quantity is consumed immediately in animal respiration, so that the animal population shows virtually no annual increase, or contribution to the net ecosystem production. The principal contribution to the net ecosystem production is the growth of the plant populations, which



square meter, some 2,100 grams are lost in respiration, leaving 550 stored as new plant growth, litter and humus. The animal population is not increasing appreciably. This is a "late successional" forest in which 80 percent of the production is expended in respiration.



RATE OF RESPIRATION of the forest was determined by measuring the rate at which carbon dioxide, a product of respiration, accumulated during nights when the air was still because of a temperature inversion. The curves give the carbon dioxide concentration at four elevations in the course of one such night. (Note that the temperature, recorded at 3:00 A.M., was lower near the ground than at greater heights.) The hourly increase in carbon dioxide concentration, which was calculated from these curves, yielded rate of respiration.



RESPIRATION of the forest, plotted against temperature, is seen to proceed at a higher rate in summer (*colored curve*) than in winter (*black curve*). Annual respiration was calculated in grams of carbon dioxide, then converted to yield the total respiration, 2,100 grams.

accounts for more than 40 percent of the net production. The remainder of the net production enters the food chains of decay, which are obviously well developed. Clearly the elimination of deer, combined with poorly developed herbivore and carnivore populations, has resulted in a diversion of energy from the grazing chain into the food chains of decay.

This is precisely what happens in aquatic systems as they are enriched with nutrients washed from the land; the shift to decay is also caused by the accumulation of any toxic substance, whether it affects plants or animals. Any reduction in populations of grazers shifts the flow of energy toward decay. Any effect on the plants shifts plant populations away from sensitive species toward resistant species that may not be food for the indigenous herbivores, thereby eliminating the normal food chains and also shifting the flow of energy into decay.

These observations simply show that the structure and function of major ecosystems are sensitive to many influences. Clearly the amount of living tissue that can be supported in any ecosystem depends on the amount of net production. Net production, however, is coupled to both photosynthesis and respiration, both of which can be affected by many factors. Photosynthesis is sensitive to light intensity and duration, to the availability of water and mineral nutrients and to temperature. It is also sensitive to the concentration of carbon dioxide; on a worldwide basis the amount of carbon dioxide in the atmosphere may exert a major control over rates of net production. Greenhouse men have recognized the sensitivity of photosynthesis to carbon dioxide concentration for many years and sometimes increase the concentration artificially to stimulate plant growth. Has the emission of carbon dioxide from the combustion of fossil fuels in the past 150 years caused a worldwide increase in net production, and if so, how much of an increase?

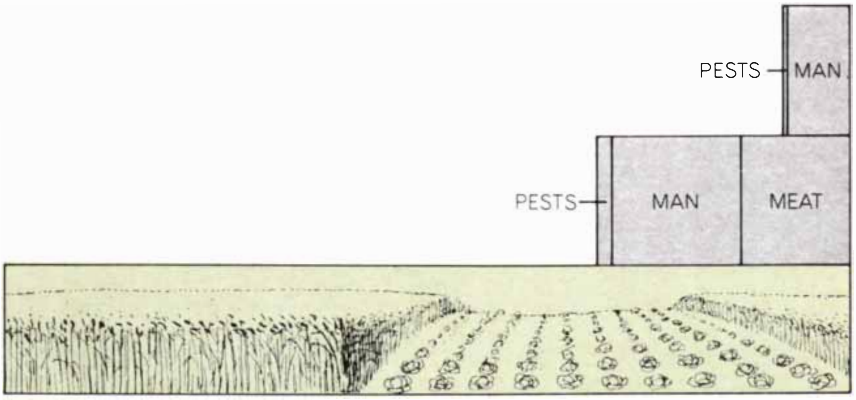
With equipment specially designed at Brookhaven, Robert Wright and I supplied air with enhanced levels of carbon dioxide to trees and determined the effect on net photosynthesis by measuring the uptake of the gas by leaves. The net amount of carbon dioxide that was fixed increased linearly with the increase in the carbon dioxide concentration in the air. Such small increases in carbon dioxide concentration have virtually no effect on rates of respiration. The data suggest that the increase of about 10 percent (30 parts per million) in the carbon dioxide concentration of the atmosphere since the middle of the 19th century caused by the industrial revolution may have increased net production by as much as 5 to 10 percent. This increase, if applicable worldwide and considered alone, would increase the total energy (and carbon) stored in natural ecosystems by an equivalent amount, and would result in an equivalent improvement in the yields of agriculture. The increase in net production also tends to stabilize the carbon dioxide content of the atmosphere by storing more carbon in living organic matter, particularly in forests, and in the nonliving organic matter of sediments and humus. Such changes have almost certainly occurred on a worldwide basis as an inadvertent result of human activities in the past 100 years or so.

Such simple single-factor analyses of environmental problems, however, are almost always misleading. As the carbon dioxide concentration in the atmosphere has been increasing, many other factors have changed. There was a period of rising temperature, possibly due to the increased carbon dioxide concentration. More recently, however, there has been a decline in world temperatures that continues. This can be expected to reduce net production worldwide by reducing the periods favorable for plant growth. Added to the effects of changing temperature—and indeed overriding it—is the accumulation of toxic wastes from human activities. The overall effect is to reduce the structure of ecosystems. This in turn shortens food chains and favors (1) populations of small hardy plants, (2) small-bodied herbivores that reproduce rapidly and (3) the food chains of decay. The loss of structure also implies a loss of "regulation"; the simplified communities are subject to rapid changes in the density of these smaller, more rapidly reproducing organisms that have been released from their normal controls.

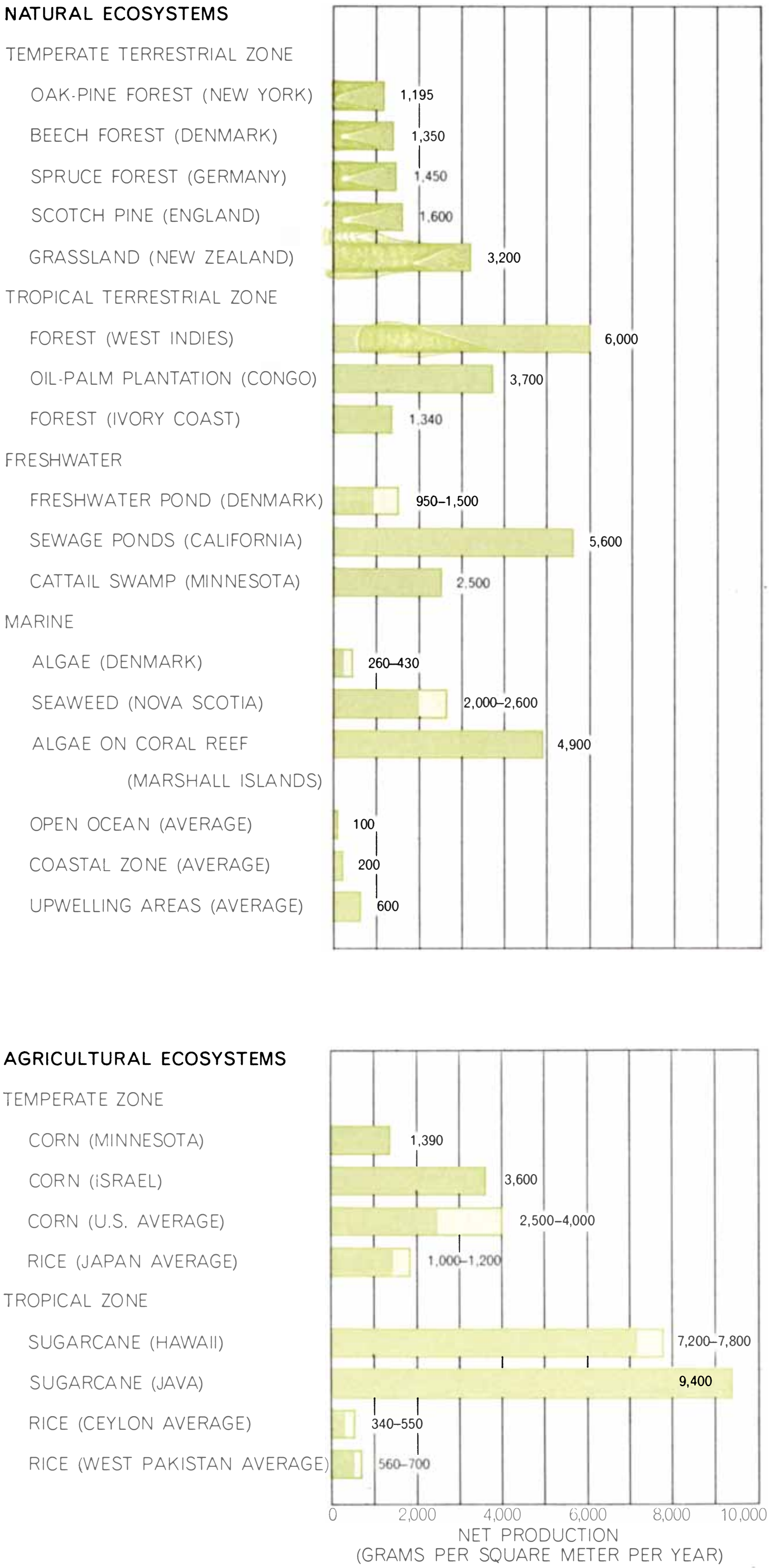
Local increases in water temperature also give rise to predictable effects. There is talk, for example, of warming the waters of the New York region with waste heat from reactors to produce a rich "tropical" biota, but such manipulation would produce a degraded local biota supplemented by a few hardy species of more southerly ecosystems. Such circumstances again favor productivity not by complex, highly integrated arrays of specialized organisms but by simple arrays of generalized ones. Energy then is funneled not into intricate food webs capped by tuna, mackerel, petrels, dolphins and other highly specialized carni-

INTACT NATURAL ECOSYSTEM is exemplified by a mature oak-hickory forest that supports several stages of consumers in the grazing food chain, with from 10 to 20 percent of the energy in each trophic level being passed along to the next level. The symbols represent different herbivore and carnivore species. Complexity of structure regulates population sizes, maintaining the same pattern of energy distribution in the system from year to year.

DEGRADED ECOSYSTEM has a truncated grazing chain. The annual production of the sparse grasses, herbs and shrubs fluctuates (*shaded area*). So do populations of herbivores and carnivores, which are characterized by large numbers of individuals but few different species. Under extreme conditions most of the net production may be consumed, leading to the starvation of herbivores and accentuating the characteristic fluctuation in populations.



AGRICULTURAL ECOSYSTEM is a special case, yielding a larger than normal harvest of net production for herbivores, including man and animals that provide meat for man. Stability is maintained through inputs of energy in cultivation, pesticides and fertilizer.



NET PRODUCTION LEVELS of a number of natural and agricultural ecosystems are compared. (The total net production of U.S. corn and of rice is calculated from grain yields.)

vores but into simple food webs dominated by hardy scavengers such as gulls and crabs and into the food webs of decay. As the annual contribution to decay increases, these webs in water become overloaded; the oxygen dissolved in the water is used up and metabolism shifts from the aerobic form where oxygen is freely available to the much less efficient anaerobic respiration; organic matter accumulates, releasing methane, hydrogen sulfide and other noxious gases that only reinforce the tendency.

The broad pattern of these changes is clear enough. On the one hand, an increasing fraction of the total energy fixed is being diverted to the direct support of man, replacing the earth's major ecosystems with cities and land devoted to agriculture—the simplified ecosystems of civilization that require continuing contributions of energy under human control for their regulation. On the other hand, the leakage of toxic substances from the man-dominated provinces of the earth is reducing the structure and self-regulation of the remaining natural ecosystems. The trend is progressive. The simplification of the earth's biota is breaking down the insulation of large units of the earth's surface, increasing the interactions between terrestrial and aquatic systems, between upland and lowland, between river and estuary. The long-term trend of evolution toward building complex, integral, stable ecosystems is being reversed. Although the changes are rapid, accelerating and important, they do not mean that the earth will face an oxygen crisis; photosynthesis will continue for a long time yet, perhaps at an accelerated rate in certain places, stimulated by increased carbon dioxide concentrations in air and the availability of nutrients in water. A smaller fraction of the earth's fixed energy is easily available to man, however. The energy flows increasingly through smaller organisms such as the hardy shrubs and herbs of the irradiated forest at Brookhaven, the scrub oaks that are replacing the smog-killed pines of the Los Angeles basin, the noxious algae of eutrophic lakes and estuaries, into short food chains, humus and anaerobic sediments.

These are major man-caused changes in the biosphere. Many aspects of them are irreversible; their implications are poorly known. Together they constitute a major series of interlocking objectives for science and society in the next decade focused on the question: "How much of the energy that runs the biosphere can be diverted to the support of a single species: man?"