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30. The following abbreviations are used in the figures and figure legends: *A*, auditory area of cortex; *CM* + *Pf*, centromedian + parafascicular nuclei; *GL*, lateral geniculate nucleus; *GM*, medial geniculate nucleus; *Hab*, habenula; *Hip*, hippocampus; *L*, lateral group of nuclei; *LP*, lateroposterior nucleus; *MD*, mediodorsal nucleus; *PC*, posterior commissure; *Po*, posterior nucleus; *Pul*, pulvinar nucleus; *R*, reticular nucleus; *S I*, somatic area I; *S II*, somatic area II; *SC*, superior colliculus; *T*, temporal area of cortex; *TO*, optic tract; *V*, ventral group; *V I*, visual area I; *V II*, visual area II; *VGL*, ventral lateral geniculate; *VL*, ventrolateral nucleus; *VM*, ventromedial nucleus; *VP*, ventroposterior nucleus; *ZI*, zona incerta.
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The Strategy of Ecosystem Development

An understanding of ecological succession provides a basis for resolving man's conflict with nature.

Eugene P. Odum

The principles of ecological succession bear importantly on the relationships between man and nature. The framework of successional theory needs to be examined as a basis for resolving man's present environmental crisis. Most ideas pertaining to the development of ecological systems are based on descriptive data obtained by observing changes in biotic communities over long periods, or on highly theoretical assumptions; very few of the generally accepted hypotheses have been tested experimentally. Some of the confusion, vagueness, and lack of experimental work in this area stems from the tendency of ecologists to regard "succession" as a single straightforward idea; in actual fact, it entails an interacting complex of processes, some of which counteract one another.

As viewed here, ecological succession involves the development of ecosystems; it has many parallels in the developmental biology of organisms, and also in the development of human society. The ecosystem, or ecological system, is considered to be a unit of biological organization made up of all of the organisms in a given area (that is, "community") interacting with the physical environment so that a flow of energy leads to characteristic trophic structure and material cycles within the system. It is the purpose of this article to summarize, in the form of a tabular model, components and stages of development at the ecosystem level as a means of emphasizing those aspects of ecological succession that can be accepted on the basis of present knowledge, those that require more study, and those that have special relevance to human ecology.

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Definition of Succession

Ecological succession may be defined in terms of the following three parameters (*1*). (i) It is an orderly process of community development that is reasonably directional and, therefore, predictable. (ii) It results from modification of the physical environment by the community; that is, succession is community-controlled even though the physical environment determines the pattern, the rate of change, and often sets limits as to how far development can go. (iii) It culminates in a stabilized ecosystem in which maximum biomass (or high information content) and symbiotic function between organisms are maintained per unit of available energy flow. In a word, the "strategy" of succession as a short-term process is basically the same as the "strategy" of long-term evolutionary development of the biosphere—namely, increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations. As I illustrate below, the strategy of "maximum protection" (that is, trying to achieve maximum support of complex biomass structure) often conflicts with man's goal of "maximum

production" (trying to obtain the highest possible yield). Recognition of the ecological basis for this conflict is, I believe, a first step in establishing rational land-use policies.

The earlier descriptive studies of succession on sand dunes, grasslands, forests, marine shores, or other sites, and more recent functional considerations, have led to the basic theory contained in the definition given above. H. T. Odum and Pinkerton (*2*), building on Lotka's (*3*) "law of maximum energy in biological systems," were the first to point out that succession involves a fundamental shift in energy flows as increasing energy is relegated to maintenance. Margalef (*4*) has recently documented this bioenergetic basis for succession and has extended the concept.

Changes that occur in major structural and functional characteristics of a developing ecosystem are listed in Table 1. Twenty-four attributes of ecological systems are grouped, for convenience of discussion, under six headings. Trends are emphasized by contrasting the situation in early and late development. The degree of absolute change, the rate of change, and the time required to reach a steady state may vary not only with different climatic and physiographic situations but also with different ecosystem attributes in the same physical environment. Where good data are available, rate-of-change curves are usually convex, with changes occurring most rapidly at the beginning, but bimodal or cyclic patterns may also occur.

Bioenergetics of Ecosystem Development

Attributes 1 through 5 in Table 1 represent the bioenergetics of the ecosystem. In the early stages of ecological succession, or in "young nature," so to speak, the rate of primary production or total (gross) photosynthesis (P) exceeds the rate of community respiration (R), so that the P/R ratio is greater than 1. In the special case of organic pollution, the P/R ratio is typically less than 1. In both cases, however, the theory is that P/R approaches 1 as succession occurs. In other words, energy fixed tends to be balanced by the energy cost of maintenance (that is, total community respiration) in the mature or "climax" ecosystem. The P/R ratio, therefore, should be an excellent functional index of the relative maturity of the system.

So long as P exceeds R, organic matter and biomass (B) will accumulate in the system (Table 1, item 6), with the result that ratio P/B will tend to decrease or, conversely, the B/P, B/R, or B/E ratios (where $E = P + R$) will increase (Table 1, items 2 and 3). Theoretically, then, the amount of standing-crop biomass supported by the available energy flow (E) increases to a maximum in the mature or climax stages (Table 1, item 3). As a consequence, the net community production, or yield, in an annual cycle is large in young nature and small or zero in mature nature (Table 1, item 4).

Comparison of Succession in a Laboratory Microcosm and a Forest

One can readily observe bioenergetic changes by initiating succession in experimental laboratory microecosystems. Aquatic microecosystems, derived from various types of outdoor systems, such as ponds, have been cultured by Beyers (*5*), and certain of these mixed cultures are easily replicated and maintain themselves in the climax state indefinitely on defined media in a flask with only light input (*6*). If samples from the climax system are inoculated into fresh media, succession occurs, the mature system developing in less than 100 days. In Fig. 1 the general pattern of a 100-day autotrophic succession in a microcosm based on data of Cooke (*7*) is compared with a hypothetical model of a 100-year forest succession as presented by Kira and Shidei (*8*).

During the first 40 to 60 days in a typical microcosm experiment, daytime net production (P) exceeds nighttime respiration (R), so that biomass (B) accumulates in the system (*9*). After an early "bloom" at about 30 days, both rates decline, and they become approximately equal at 60 to 80 days. the B/P ratio, in terms of grams of carbon supported per gram of daily carbon production, increases from less than 20 to more than 100 as the steady state is reached. Not only are autotrophic and heterotrophic metabolism balanced in the climax, but a large organic structure is supported by small daily production and respiratory rates.

While direct projection from the small laboratory microecosystem to open nature may not be entirely valid, there is evidence that the same basic trends that are seen in the laboratory are characteristic of succession on land and in large bodies of water. Seasonal successions also often follow the same pattern, an early seasonal bloom characterized by rapid growth of a few dominant species being followed by the development later in the season of high B/P ratios, increased diversity, and a relatively steady, if temporary, state in terms of P and R (*4*). Open systems may not experience a decline, at maturity, in total or gross productivity, as the space-limited microcosms do, but the general pattern of bioenergetic change in the latter seems to mimic nature quite well.

These trends are not, as might at first seem to be the case, contrary to the classical limnological teaching which describes lakes as progressing in time from the less productive (oligotrophic) to the more productive (eutrophic) state. Table 1, as already emphasized, refers to changes which are brought about by biological processes *within* the ecosystem in question. Eutrophication, whether natural or cultural, results when nutrients are imported into the lake from *outside* the lake—that is, from the watershed. This is equivalent to adding nutrients to the laboratory microecosystem or fertilizing a field; the system is pushed back, in successional terms, to a younger or "bloom" state. Recent studies on lake sediments (*10*), as well as theoretical considerations (*11*), have indicated that lakes can and do progress to a more oligotrophic condition when the nutrient input from the watershed slows or ceases. Thus, there is hope that the troublesome cultural eutrophication of our waters can be reversed if the inflow of nutrients from the watershed can be greatly reduced. Most of all, however, this situation emphasizes that it is the entire drainage or catchment basin, not just the lake or stream, that must be considered the ecosystem unit if we are to deal successfully with our water pollution problems. Ecosystematic study of entire landscape catchment units is a major goal of the American plan for the proposed International Biological Program. Despite the obvious logic of such a proposal, it is proving surprisingly difficult to get tradition-bound scientists and granting agencies to look beyond their specialties toward the support of functional studies of large units of the landscape.

Food Chains and Food Webs

As the ecosystem develops, subtle changes in the network pattern of food chains may be expected. The manner in which organisms are linked together through food tends to be relatively sim-

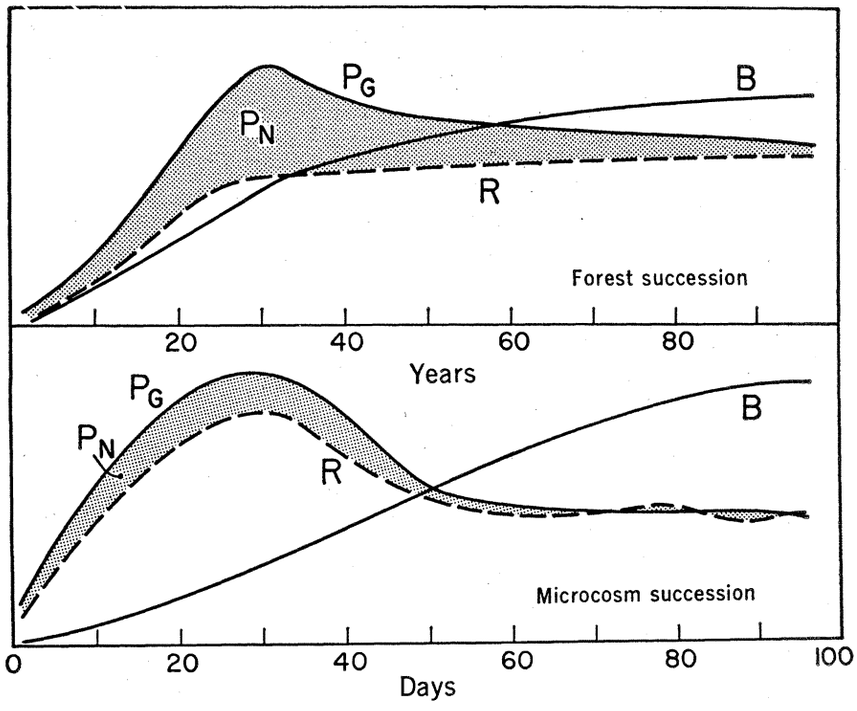


Fig. 1. Comparison of the energetics of succession in a forest and a laboratory microcosm. P_G, gross production; P_N, net production; R, total community respiration; B, total biomass.

ple and linear in the very early stages of succession, as a consequence of low diversity. Furthermore, heterotrophic utilization of net production occurs predominantly by way of grazing food chains—that is, plant-herbivore-carnivore sequences. In contrast, food chains become complex webs in mature stages, with the bulk of biological energy flow following detritus pathways (Table 1, item 5). In a mature forest, for example, less than 10 percent of annual net production is consumed (that is, grazed) in the living state (*12*); most is utilized as dead matter (detritus) through delayed and complex pathways involving as yet little understood animal-microorganism interactions. The time involved in an uninterrupted succession allows for increasingly intimate associations and reciprocal adaptations between plants and animals, which lead to the development of many mechanisms that reduce grazing—such as the development of indigestible supporting tissues (cellulose, lignin, and so on), feedback control between plants and herbivores (*13*), and increasing predatory pressure on herbivores (*14*). Such mechanisms enable the biological community to maintain the large and complex organic structure that mitigates perturbations of the physical environment. Severe stress or rapid changes brought about by outside forces can of course, rob the system of these protective mechanisms and allow irruptive, cancerous growths of certain species to occur, as man too often finds to his sorrow. An example of a stress-induced pest irruption occurred at Brookhaven National Laboratory, where oaks became vulnerable to aphids when translocation of sugars and amino acids was impaired by continuing gamma irradiation (*15*).

Radionuclide tracers are providing a means of charting food chains in the intact outdoor ecosystem to a degree that will permit analysis within the concepts of network or matrix algebra. For example, we have recently been able to map, by use of a radiophosphorus tracer, the open, relatively linear food linkage between plants and insects in an early old-field successional stage (*16*).

Diversity and Succession

Perhaps the most controversial of the successional trends pertain to the complex and much discussed subject of diversity (*17*). It is important to distinguish between different kinds of diversity indices, since they may not follow parallel trends in the same gradient or developmental series. Four components of diversity are listed in Table 1, items 8 through 11.

The variety of species, expressed as a species-number ratio or a species-area ratio, tends to increase during the early stages of community development. A second component of species diversity is what has been called equitability, or evenness (*18*), in the apportionment of individuals among the species. For example, two systems each containing 10 species and 100 individuals have the same diversity in terms of species-number ratio but could have widely different equitabilities depending on the apportionment of the 100 individuals among the 10 species—for example, 91-1-1-1-1-1-1-1-1-1 at one extreme or 10 individuals per species at the other. The Shannon formula,

$$-\Sigma \frac{ni}{N} \log_2 \frac{ni}{N}$$

where ni is the number of individuals in each species and N is the total number of individuals, is widely used as a diversity index because it combines the variety and equitability components in one approximation. But, like all such lumping parameters, Shannon's formula may obscure the behavior of these two rather different aspects of diversity. For example, in our most recent field experiments, an acute stress from insecticide reduced the number of species of insects relative to the number of individuals but increased the evenness in the relative abundances of the surviving species (*19*). Thus, in this case the "variety" and "evenness" components would tend to cancel each other in Shannon's formula.

While an increase in the variety of species together with reduced dominance by any one species or small group of species (that is, increased evenness) can be accepted as a general probability during succession (*20*), there are other community changes that may work against these trends. An increase in the size of organisms, an increase in the length and complexity of life histories, and an increase in interspecific competition that may result in competitive exclusion of species (Table 1, items 12–14) are trends that may reduce the number of species that can live in a given area. In the bloom stage of succession organisms tend to be small and to have simple life histories and rapid rates of reproduction. Changes in size appear to be a consequence of, or an adaptation to, a shift in nutrients from inorganic to organic (Table 1, item 7). In a mineral nutrient-rich environment, small size is of selective advantage, especially to autotrophs, because of the greater surface-to-volume ratio. As the

ecosystem develops, however, inorganic nutrients tend to become more and more tied up in the biomass (that is, to become intrabiotic), so that the selective advantage shifts to larger organisms (either larger individuals of the same species or larger species, or both) which have greater storage capacities and more complex life histories, thus are adapted to exploiting seasonal or periodic releases of nutrients or other resources. The question of whether the seemingly direct relationship between organism size and stability is the result of positive feedback or is merely fortuitous remains unanswered (*21*).

Thus, whether or not species diversity continues to increase during succession will depend on whether the increase in potential niches resulting from increased biomass, stratification (Table 1, item 9), and other consequences of biological organization exceeds the countereffects of increasing size and competition. No one has yet been able to catalogue all the species in any sizable area, much less follow total species diversity in a successional series. Data are so far available only for segments of the community (trees, birds, and so on). Margalef (*4*) postulates that diversity will tend to peak during the early or middle stages of succession and then decline in the climax. In a study of bird populations along a successional gradient we found a bimodal pattern (*22*); the number of species increased during the early stages of old-field succession, declined during the early forest stages, and then increased again in the mature forest.

Species variety, equitability, and stratification are only three aspects of diversity which change during succession. Perhaps an even more important trend is an increase in the diversity of organic compounds, not only of those within the biomass but also of those excreted and secreted into the media (air, soil, water) as by-products of the increasing community metabolism. An increase in such "biochemical diversity" (Table 1, item 10) is illustrated by the increase in the variety of plant pigments along a successional gradient in aquatic situations, as described by Margalef (*4*, *23*). Biochemical diversity within populations, or within systems as a whole, has not yet been systematically studied to the degree the subject of species diversity has been. Consequently, few generalizations can be made, except that it seems safe to say that, as succession progresses, organic extrametabolites probably serve increasingly important functions as regulators which stabilize the growth and composition of the ecosystem. Such metabolites may, in fact, be extremely important in preventing populations from overshooting the equilibrial density, thus in reducing oscillations as the system develops stability.

The cause-and-effect relationship between diversity and stability is not clear and needs to be investigated from many angles. If it can be shown that biotic diversity does indeed enhance physical stability in the ecosystem, or is the result of it, then we would have an important guide for conservation practice. Preservation of hedgerows, woodlots, noneconomic species, noneutrophicated waters, and other biotic variety in man's landscape could then be justified on scientific as well as esthestic grounds, even though such preservation often must result in some reduction in the production of food or other immediate consumer needs. In other words, is variety only the spice of life, or is it a necessity for the long life of the total ecosystem comprising man and nature?

Nutrient Cycling

An important trend in successional development is the closing or "tightening" of the biogeochemical cycling of major nutrients, such as nitrogen, phosphorus, and calcium (Table 1, items 15–17). Mature systems, as compared to developing ones, have a greater capacity to entrap and hold nutrients for cycling within the system. For example, Bormann and Likens (*24*) have estimated that only 8 kilograms per hectare out of a total pool of exchangeable calcium of 365 kilograms per hectare is lost per year in stream outflow from a North Temperate watershed covered with a mature forest. Of this, about 3 kilograms per hectare is replaced by rainfall, leaving only 5 kilograms to be obtained from weathering of the underlying rocks in order for the system to maintain mineral balance. Reducing the volume of the vegetation, or otherwise setting the succession back to a younger state, results in increased water yield by way of stream outflow (*25*), but this

Table 1. A tabular model of ecological succession: trends to be expected in the development of ecosystems.

Ecosystem attributes	Developmental stages	Mature stages
Community energetics		
1. Gross production/community respiration (P/R ratio)	Greater or less than 1	Approaches 1
2. Gross production/standing crop biomass (P/B ratio)	High	Low
3. Biomass supported/unit energy flow (B/E ratio)	Low	High
4. Net community production (yield)	High	Low
5. Food chains	Linear, predominantly grazing	Weblike, predominantly detritus
Community structure		
6. Total organic matter	Small	Large
7. Inorganic nutrients	Extrabiotic	Intrabiotic
8. Species diversity—variety component	Low	High
9. Species diversity—equitability component	Low	High
10. Biochemical diversity	Low	High
11. Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well-organized
Life history		
12. Niche specialization	Broad	Narrow
13. Size of organism	Small	Large
14. Life cycles	Short, simple	Long, complex
Nutrient cycling		
15. Mineral cycles	Open	Closed
16. Nutrient exchange rate, between organisms and environment	Rapid	Slow
17. Role of detritus in nutrient regeneration	Unimportant	Important
Selection pressure		
18. Growth form	For rapid growth ("r-selection")	For feedback control ("K-selection")
19. Production	Quantity	Quality
Overall homeostasis		
20. Internal symbiosis	Undeveloped	Developed
21. Nutrient conservation	Poor	Good
22. Stability (resistance to external perturbations)	Poor	Good
23. Entropy	High	Low
24. Information	Low	High

greater outflow is accompanied by greater losses of nutrients, which may also produce downstream eutrophication. Unless there is a compensating increase in the rate of weathering, the exchangeable pool of nutrients suffers gradual depletion (not to mention possible effects on soil structure resulting from erosion). High fertility in "young systems" which have open nutrient cycles cannot be maintained without compensating inputs of new nutrients; examples of such practice are the continuous-flow culture of algae, or intensive agriculture where large amounts of fertilizer are imported into the system each year.

Because rates of leaching increase in a latitudinal gradient from the poles to the equator, the role of the biotic community in nutrient retention is especially important in the high-rainfall areas of the subtropical and tropical latitudes, including not only land areas but also estuaries. Theoretically, as one goes equatorward, a larger percentage of the available nutrient pool is tied up in the biomass and a correspondingly lower percentage is in the soil or sediment. This theory, however, needs testing, since data to show such a geographical trend are incomplete. It is perhaps significant that conventional North Temperate row-type agriculture, which represents a very youthful type of ecosystem, is successful in the humid tropics only if carried out in a system of "shifting agriculture" in which the crops alternate with periods of natural vegetative redevelopment. Tree culture and the semiaquatic culture of rice provide much better nutrient retention and consequently have a longer life expectancy on a given site in these warmer latitudes.

Selection Pressure: Quantity versus Quality

MacArthur and Wilson (*26*) have reviewed stages of colonization of islands which provide direct parallels with stages in ecological succession on continents. Species with high rates of reproduction and growth, they find, are more likely to survive in the early uncrowded stages of island colonization. In contrast, selection pressure favors species with lower growth potential but better capabilities for competitive survival under the equilibrium density of late stages. Using the terminology of growth equations, where r is the intrinsic rate of increase and K is the upper asymptote or equilibrium population size, we may say that "r selection" predominates in early colonization, with "K selection" prevailing as more and more species and individuals attempt to colonize (Table 1, item 18). The same sort of thing is even seen within the species in certain "cyclic" northern insects in which "active" genetic strains found at low densities are replaced at high densities by "sluggish" strains that are adapted to crowding (*27*).

Genetic changes involving the whole biota may be presumed to accompany the successional gradient, since, as described above, quantity production characterizes the young ecosystem while quality production and feedback control are the trademarks of the mature system (Table 1, item 19). Selection at the ecosystem level may be primarily interspecific, since species replacement is a characteristic of successional series or seres. However, in most well-studied seres there seem to be a few early successional species that are able to persist through to late stages. Whether genetic changes contribute to adaptation in such species has not been determined, so far as I know, but studies on population genetics of *Drosophila* suggest that changes in genetic composition could be important in population regulation (*28*). Certainly, the human population, if it survives beyond its present rapid growth stage, is destined to be more and more affected by such selection pressures as adaptation to crowding becomes essential.

Overall Homeostasis

This brief review of ecosystem development emphasizes the complex nature of processes that interact. While one may well question whether all the trends described are characteristic of all types of ecosystems, there can be little doubt that the net result of community actions is symbiosis, nutrient conservation, stability, a decrease in entropy, and an increase in information (Table 1, items 20–24). The overall strategy is, as I stated at the beginning of this article, directed toward achieving as large and diverse an organic structure as is possible within the limits set by the available energy input and the prevailing physical conditions of existence (soil, water, climate, and so on). As studies of biotic communities become more functional and sophisticated, one is impressed with the importance of mutualism, parasitism, predation, commensalism, and other forms of symbiosis. Partnership between unrelated species is often noteworthy (for example, that between coral coelenterates and algae, or between mycorrhizae and trees). In many cases, at least, biotic control of grazing, population density, and nutrient cycling provide the chief positive-feedback mechanisms that contribute to stability in the mature system by preventing overshoots and destructive oscillations. The intriguing question is, Do mature ecosystems age, as organisms do? In other words, after a long period of relative stability or "adulthood," do ecosystems again develop unbalanced metabolism and become more vulnerable to diseases and other perturbations?

Relevance of Ecosystem Development Theory to Human Ecology

Figure 1 depicts a basic conflict between the strategies of man and of nature. The "bloom-type" relationships, as exhibited by the 30-day microcosm or the 30-year forest, illustrate man's present idea of how nature should be directed. For example, the goal of agriculture or intensive forestry, as now generally practiced, is to achieve high rates of production of readily harvestable products with little standing crop left to accumulate on the landscape—in other words, a high P/B efficiency. Nature's strategy, on the other hand, as seen in the outcome of the successional process, is directed toward the reverse efficiency—a high B/P ratio, as is depicted by the relationship at the right in Fig. 1. Man has generally been preoccupied with obtaining as much "production" from the landscape as possible, by developing and maintaining early successional types of ecosystems, usually monocultures. But, of course, man does not live by food and fiber alone; he also needs a balanced CO_2–O_2 atmosphere, the climatic buffer provided by oceans and masses of vegetation, and clean (that is, unproductive) water for cultural and industrial uses. Many essential life-cycle resources, not to mention recreational and esthetic needs, are best provided man by the less "productive" landscapes. In other words, the landscape is not just a supply depot but is also the *oikos*—the home—in which we must live. Until recently mankind has more or less taken for granted the

gas-exchange, water-purification, nutrient-cycling, and other protective functions of self-maintaining ecosystems, chiefly because neither his numbers nor his environmental manipulations have been great enough to affect regional and global balances. Now, of course, it is painfully evident that such balances are being affected, often detrimentally. The "one problem, one solution approach" is no longer adequate and must be replaced by some form of ecosystem analysis that considers man as a part of, not apart from, the environment.

The most pleasant and certainly the safest landscape to live in is one containing a variety of crops, forests, lakes, streams, roadsides, marshes, seashores, and "waste places"—in other words, a mixture of communities of different ecological ages. As individuals we more or less instinctively surround our houses with protective, nonedible cover (trees, shrubs, grass) at the same time that we strive to coax extra bushels from our cornfield. We all consider the cornfield a "good thing," of course, but most of us would not want to live there, and it would certainly be suicidal to cover the whole land area of the biosphere with cornfields, since the boom and bust oscillation in such a situation would be severe.

The basic problem facing organized society today boils down to determining in some objective manner when we are getting "too much of a good thing." This is a completely new challenge to mankind because, up until now, he has had to be concerned largely with too little rather than too much. Thus, concrete is a "good thing," but not if half the world is covered with it. Insecticides are "good things," but not when used, as they now are, in an indiscriminate and wholesale manner. Likewise, water impoundments have proved to be very useful man-made additions to the landscape, but obviously we don't want the whole country inundated! Vast man-made lakes solve some problems, at least temporarily, but yield comparative little food or fiber, and, because of high evaporative losses, they may not even be the best device for storing water; it might better be stored in the watershed, or underground in aquafers. Also, the cost of building large dams is a drain on already overtaxed revenues. Although as individuals we readily recognize that we can have too many dams or other large-scale environmental changes, governments are so fragmented and lacking in systems-analysis capabilities that there is no effective mechanism whereby negative feedback signals can be received and acted on before there has been a serious overshoot. Thus, today there are governmental agencies, spurred on by popular and political enthusiasm for dams, that are putting on the drawing boards plans for damming every river and stream in North America!

Table 2. Contrasting characteristics of young and mature-type ecosystems.

Young	Mature
Production	Protection
Growth	Stability
Quantity	Quality

Society needs, and must find as quickly as possible, a way to deal with the landscape as a whole, so that manipulative skills (that is, technology) will not run too far ahead of our understanding of the impact of change. Recently a national ecological center outside of government and a coalition of governmental agencies have been proposed as two possible steps in the establishment of a political control mechanism for dealing with major environmental questions. The soil conservation movement in America is an excellent example of a program dedicated to the consideration of the whole farm or the whole watershed as an ecological unit. Soil conservation is well understood and supported by the public. However, soil conservation organizations have remained too exclusively farm-oriented, and have not yet risen to the challenge of the urban-rural landscape, where lie today's most serious problems. We do, then, have potential mechanisms in American society that could speak for the ecosystem as a whole, but none of them are really operational (*29*).

The general relevance of ecosystem development theory to landscape planning can, perhaps, be emphasized by the "mini-model" of Table 2, which contrasts the characteristics of young and mature-type ecosystems in more general terms than those provided by Table 1. It is mathematically impossible to obtain a maximum for more than one thing at a time, so one cannot have both extremes at the same time and place. Since all six characteristics listed in Table 2 are desirable in the aggregate, two possible solutions to the dilemma immediately suggest themselves. We can compromise so as to provide moderate quality and moderate yield on all the landscape, or we can deliberately plan to compartmentalize the landscape so as to simultaneously maintain highly productive and predominantly protective types as separate units subject to different management strategies (strategies ranging, for example, from intensive cropping on the one hand to wilderness management on the other). If ecosystem development theory is valid and applicable to planning, then the so-called multiple-use strategy, about which we hear so much, will work only through one or both of these approaches, because, in most cases, the projected multiple uses conflict with one another. It is appropriate, then, to examine some examples of the compromise and the compartmental strategies.

Pulse Stability

A more or less regular but acute physical perturbation imposed from without can maintain an ecosystem at some intermediate point in the developmental sequence, resulting in, so to speak, a compromise between youth and maturity. What I would term "fluctuating water level ecosystems" are good examples. Estuaries, and intertidal zones in general, are maintained in an early, relatively fertile stage by the tides, which provide the energy for rapid nutrient cycling. Likewise, freshwater marshes, such as the Florida Everglades, are held at an early successional stage by the seasonal fluctuations in water levels. The dry-season drawdown speeds up aerobic decomposition of accumulated organic matter, releasing nutrients that, on reflooding, support a wet-season bloom in productivity. The life histories of many organisms are intimately coupled to this periodicity. The wood stork, for example, breeds when the water levels are falling and the small fish on which it feeds become concentrated and easy to catch in the drying pools. If the water level remains high during the usual dry season or fails to rise in the wet season, the stork will not nest (*30*). Stabilizing water levels in the Everglades by means of dikes, locks, and impoundments, as is now advocated by some, would, in my opinion, destroy rather than preserve the Everglades as we now know them just as surely as complete drainage would. Without periodic drawdowns and fires, the shallow basins would fill up with organic matter and

succession would proceed from the present pond-and-prairie condition toward a scrub or swamp forest.

It is strange that man does not readily recognize the importance of recurrent changes in water level in a natural situation such as the Everglades when similar pulses are the basis for some of his most enduring food culture systems (*31*). Alternate filling and draining of ponds has been a standard procedure in fish culture for centuries in Europe and the Orient. The flooding, draining, and soil-aeration procedure in rice culture is another example. The rice paddy is thus the cultivated analogue of the natural marsh or the intertidal ecosystem.

Fire is another physical factor whose periodicity has been of vital importance to man and nature over the centuries. Whole biotas, such as those of the African grasslands and the California chaparral, have become adapted to periodic fires producing what ecologists often call "fire climaxes" (*32*). Man uses fire deliberately to maintain such climaxes or to set back succession to some desired point. In the southeastern coastal plain, for example, light fires of moderate frequency can maintain a pine forest against the encroachment of older successional stages which, at the present time at least, are considered economically less desirable. The fire-controlled forest yields less wood than a tree farm does (that is, young trees, all of about the same age, planted in rows and harvested on a short rotation schedule), but it provides a greater protective cover for the landscape, wood of higher quality, and a home for game birds (quail, wild turkey, and so on) which could not survive in a tree farm. The fire climax, then, is an example of a compromise between production simplicity and protection diversity.

It should be emphasized that pulse stability works only if there is a complete community (including not only plants but animals and microorganisms) adapted to the particular intensity and frequency of the perturbation. Adaptation—operation of the selection process—requires times measurable on the evolutionary scale. Most physical stresses introduced by man are too sudden, too violent, or too arrhythmic for adaptation to occur at the ecosystem level, so severe oscillation rather than stability results. In many cases, at least, modification of naturally adapted ecosystems for cultural purposes would seem preferable to complete redesign.

Prospects for a Detritus Agriculture

As indicated above, heterotrophic utilization of primary production in mature ecosystems involves largely a delayed consumption of detritus. There is no reason why man cannot make greater use of detritus and thus obtain food or other products from the more protective type of ecosystem. Again, this would represent a compromise, since the short-term yield could not be as great as the yield obtained by direct exploitation of the grazing food chain. A detritus agriculture, however, would have some compensating advantages. Present agricultural strategy is based on selection for rapid growth and edibility in food plants, which, of course, make them vulnerable to attack by insects and disease. Consequently, the more we select for succulence and growth, the more effort we must invest in the chemical control of pests; this effort, in turn, increases the likelihood of our poisoning useful organisms, not to mention ourselves. Why not also practice the reverse strategy—that is, select plants which are essentially unpalatable, or which produce their own systemic insecticides while they are growing, and then convert the net production into edible products by microbial and chemical enrichment in food factories? We could then devote our biochemical genius to the enrichment process instead of fouling up our living space with chemical poisons! The production of silage by fermentation of low-grade fodder is an example of such a procedure already in widespread use. The cultivation of detritus-eating fishes in the Orient is another example.

By tapping the detritus food chain man can also obtain an appreciable harvest from many natural systems without greatly modifying them or destroying their protective and esthetic value. Oyster culture in estuaries is a good example. In Japan, raft and long-line culture of oysters has proved to be a very practical way to harvest the natural microbial products of estuaries and shallow bays. Furukawa (*33*) reports that the yield of cultured oysters in the Hiroshima Prefecture has increased tenfold since 1950, and that the yield of oysters (some 240,000 tons of meat) from this one district alone in 1965 was ten times the yield of natural oysters from the entire country. Such oyster culture is feasible along the entire Atlantic and Gulf coasts of the United States. A large investment in the culture of oysters and other seafoods would also provide the best possible deterrent against pollution, since the first threat of damage to the pollution-sensitive oyster industry would be immediately translated into political action!

The Compartment Model

Successful though they often are, compromise systems are not suitable nor desirable for the whole landscape. More emphasis needs to be placed on compartmentalization, so that growth-type, steady-state, and intermediate-type ecosystems can be linked with urban and industrial areas for mutual benefit. Knowing the transfer coefficients that define the flow of energy and the movement of materials and organisms (including man) between compartments, it should be possible to determine, through analog-computer manipulation, rational limits for the size and capacity of each compartment. We might start, for example, with a simplified model, shown in Fig. 2, consisting of four compartments of equal area, partitioned according to the basic biotic-function criterion—that is, according to whether the area is (i) productive, (ii) protective, (iii) a compromise between (i) and (ii) or (iv), urban-industrial. By continually refining the transfer coefficients on the basis of real world situations, and by increasing and decreasing the size and capacity of each compartment through computer simulation, it would be possible to determine objectively the limits that must eventually be imposed on each compartment in order to maintain regional and global balances in the exchange of vital energy and of materials. A systems-analysis procedure provides at least one approach to the solution of the basic dilemma posed by the question "How do we determine when we are getting too much of a good thing?" Also it provides a means of evaluating the energy drains imposed on ecosystems by pollution, radiation, harvest, and other stresses (*34*).

Implementing any kind of compartmentalization plan, of course, would require procedures for zoning the landscape and restricting the use of some land and water areas. While the principle of zoning in cities is universally accepted, the procedures now followed do not work very well because zoning restrictions are too easily overturned by

short-term economic and population pressures. Zoning the landscape would require a whole new order of thinking. Greater use of legal measures providing for tax relief, restrictions on use, scenic easements, and public ownership will be required if appreciable land and water areas are to be held in the "protective" categories. Several states (for example, New Jersey and California), where pollution and population pressure are beginning to hurt, have made a start in this direction by enacting "open space" legislation designed to get as much unoccupied land as possible into a "protective" status so that future uses can be planned on a rational and scientific basis. The United States as a whole is fortunate in that large areas of the country are in national forests, parks, wildlife refuges, and so on. The fact that such areas, as well as the bordering oceans, are not quickly exploitable gives us time for the accelerated ecological study and programming needed to determine what proportions of different types of landscape provide a safe balance between man and nature. The open oceans, for example, should forever be allowed to remain protective rather than productive territory, if Alfred Redfield's (*35*) assumptions are correct. Redfield views the oceans, the major part of the hydrosphere, as the biosphere's governor, which slows down and controls the rate of decomposition and nutrient regeneration, thereby creating and maintaining the highly aerobic terrestrial environment to which the higher forms of life, such as man, are adapted. Eutrophication of the ocean in a last-ditch effort to feed the populations of the land could well have an adverse effect on the oxygen reservoir in the atmosphere.

Until we can determine more precisely how far we may safely go in expanding intensive agriculture and urban sprawl at the expense of the protective landscape, it will be good insurance to hold inviolate as much of the latter as possible. Thus, the preservation of natural areas is not a peripheral luxury for society but a capital investment from which we expect to draw interest. Also, it may well be that restrictions in the use of land and water are our only practical means of avoiding overpopulation or too great an exploitation of resources, or both. Interestingly enough, restriction of land use is the analogue of a natural behavioral control mechanism known as "territoriality" by which many species of animals avoid crowding and social stress (*36*).

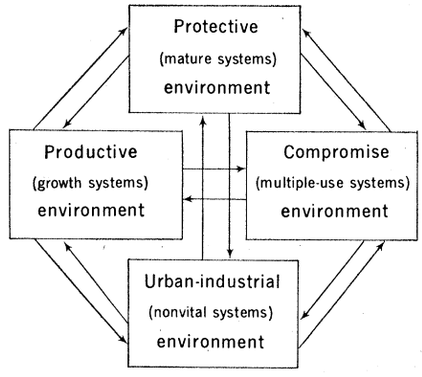


Fig. 2. Compartment model of the basic kinds of environment required by man, partitioned according to ecosystem development and life-cycle resource criteria.

Since the legal and economic problems pertaining to zoning and compartmentalization are likely to be thorny, I urge law schools to establish departments, or institutes, of "landscape law" and to start training "landscape lawyers" who will be capable not only of clarifying existing procedures but also of drawing up new enabling legislation for consideration by state and national governing bodies. At present, society is concerned—and rightly so—with human rights, but environmental rights are equally vital. The "one man one vote" idea is important, but so also is a "one man one hectare" proposition.

Education, as always, must play a role in increasing man's awareness of his dependence on the natural environment. Perhaps we need to start teaching the principles of ecosystem in the third grade. A grammar school primer on man and his environment could logically consist of four chapters, one for each of the four essential kinds of environment, shown diagrammatically in Fig. 2.

Of the many books and articles that are being written these days about man's environmental crisis, I would like to cite two that go beyond "crying out in alarm" to suggestions for bringing about a reorientation of the goals of society. Garrett Hardin, in a recent article in *Science* (*37*), points out that, since the optimum population density is less than the maximum, there is no strictly technical solution to the problem of pollution caused by overpopulation; a solution, he suggests, can only be achieved through moral and legal means of "mutual coercion, mutually agreed upon by the majority of people." Earl F. Murphy, in a book entitled *Governing Nature* (*38*), emphasizes that the regulatory approach alone is not enough to protect life-cycle resources, such as air and water, that cannot be allowed to deteriorate. He discusses permit systems, effluent charges, receptor levies, assessment, and cost-internalizing procedures as economic incentives for achieving Hardin's "mutually agreed upon coercion."

It goes without saying that the tabular model for ecosystem development which I have presented here has many parallels in the development of human society itself. In the pioneer society, as in the pioneer ecosystem, high birth rates, rapid growth, high economic profits, and exploitation of accessible and unused resources are advantageous, but, as the saturation level is approached, these drives must be shifted to considerations of symbiosis (that is, "civil rights," "law and order," "education," and "culture"), birth control, and the recycling of resources. A balance between youth and maturity in the socio-environmental system is, therefore, the really basic goal that must be achieved if man as a species is to successfully pass through the present rapid-growth stage, to which he is clearly well adapted, to the ultimate equilibrium-density stage, of which he as yet shows little understanding and to which he now shows little tendency to adapt.

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Visual Receptors and Retinal Interaction

Haldan Keffer Hartline

The neuron is the functional as well as the structural unit of the nervous system. Neurophysiology received an impetus of far-reaching effect in the 1920's, when Adrian and his colleagues developed and exploited methods for recording the activity of single neurons and sensory receptors. Adrian and Bronk were the first to analyze motor function by recording the activity of single fibers dissected from a nerve trunk and Adrian and Zotterman the first to elucidate properties of single sensory receptors (*1*). These studies laid the foundations for the unitary analysis of nervous function.

My early interest in vision was spurred by another contribution from Adrian's laboratory: his study, with R. Matthews, of the massed discharge of nerve impulses in the eel's optic nerve (*2*). I aspired to the obvious extension of this study: application of unitary analysis to the receptors and neurons of the visual system.

Oscillograms of the action potentials in a single nerve fiber are now commonplace. The three shown in Fig. 1 are from an optic nerve fiber whose retinal receptor was stimulated by light, the relative values of which are given at the left of each record. One of the earliest results of unitary analysis was to show that higher intensities are signaled by higher frequencies of discharge of uniform nerve impulses.

In 1931, when C. H. Graham and I sought to apply to an optic nerve the technique developed by Adrian and Bronk for isolating a single fiber, we made a fortunate choice of experimental animal (*3*). The xiphosuran arachnoid, *Limulus polyphemus,* commonly called "Horseshoe crab," abounds on the eastern coast of North America (*4*). These "living fossils" have lateral compound eyes that are coarsely faceted and connected to the brain by long optic nerves. The optic nerve in the adults can be frayed into thin bundles which are easy to split until just one active fiber remains. The records in Fig. 1 were obtained from such a preparation.

The sensory structures in the eye of *Limulus* from which the optic nerve fibers arise are clusters of receptor cells, arranged radially around the dendritic process of a bipolar neuron (eccentric cell) (*5*). Each cluster lies behind its corneal facet and crystalline cone, which give it its own, small visual field (Fig. 2). Each such ommatidium, though not as simple as I once thought, seems to act as a functional receptor unit. Restriction of the stimulating light to one facet elicits discharge in one fiber—the axon of the bipolar neuron

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The author is professor of biophysics at the Rockefeller University in New York City. This article is the lecture he delivered in Stockholm, Sweden, 12 December 1967, when, with Regnar Arthur Granit and George Wald, he received the Nobel Prize in medicine or physiology. It is published here with the permission of the Nobel Foundation and also is included in the complete volume of *Les Prix Nobel en 1967*, as well as in the series Nobel Lectures (in English), published by the Elsevier Publishing Company, Amsterdam and New York.