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Ecological Tools and Their Use

Man and the Ecosystem

Howard T. Odum

With vast flows of energy man now begins to possess the ecosystems that spawned him. The suburban forest of Connecticut, which once nursed Pilgrim America, and the green bays of Texas, which nourished Karankawa Indians with shellfish, are such systems suddenly under energy control and management by man.

A forest with man's energy subsidies is still an ecosystem, but the combinations of flux are new and the steady states which will prevail are little known. Conversely, the specifications of inputs and outputs necessary to produce preplanned environments are little known. A new enterprise, ecological engineering, is required to fashion synthetic systems partly under old energy budgets of nature and partly with special power take-off from civilization.

How can we provide guides and know-how for the new enterprises? What are man's tastes in ecosystems? What kinds of action can couple available energy to his tastes? Are his tastes energetic hangovers, potentially lethal? What are the formulae and the costs? Consider some general features of ecosystems, energy, matter, and man.

METHODOLOGY OF ECOSYSTEM STUDY, DEFINITIONS, AND EXAMPLES

The flows of energy and matter in the ecosystem, whether involving man or not, involve some basic definitions and principles long used for study and manipulations of small and simple ecosystems, mainly of aquatic type. The problems of the suburban forest and the Texas bays do not differ in abstraction regarding flow of matter and energy. By considering first an example from a synthetic system that somewhat simplifies the problem of a Texas bay, and then considering some preliminary efforts to make similar measurements in a forest system, the methodology of the ecosystem approach may be indicated.

The Oyster Reef System

In Figure 1 is a concrete pond ecosystem. In broad areas exposed to the sun, plankton are photosynthesizing and on a reef a concentration of consumers are respiring a considerable fraction of the system's

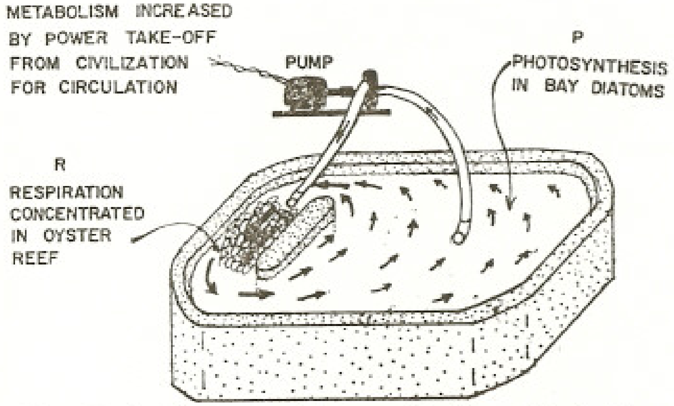

Figure 1. Synthetic system of oyster reef and bay phytoplankton, one of three units recently built of concrete.

metabolism, using the plankton for food and releasing the inorganic nutrients to the plankton. The small ratio of reef area to the larger bay area resembles the upper, low-salinity areas of the bays of the Gulf of Mexico. Whereas wind and tidal driven currents supply the necessary circulation of food to the reef and carry nutrients back to the broad bay areas, in the small, synthetic, tank system, a pump does this work with electrical energy, a power take-off from man's civilization.

By measuring changes of oxygen and carbon dioxide hourly, rates of total photosynthesis and respiration are computed; then the ratio of the processes P and R can be compared (Odum and Hoskin, 1958). Three sets of such experiments show that after initial imbalances, the metabolisms approach a steady state as long as there are no changes in regular fluxes of material. The data of Figure 2 show a flux pattern classified somewhere between the balanced case in Figure 4c and the yield system in Figure 4d where oyster growth is comparable to the timber removal.

Recently three new concrete ponds were constructed like that in Figure 1. Multiple seeding at first caused the populations in the tanks to develop differently with different species in dominant ascendency in the plankton. Then we arranged the pumps and tanks in series so that they were intermixed for several days. As in early experiences with aquarium microcosms the mixing treatment causes the systems to develop similarly. Multiple seeding followed by mixing so as to attain replications is the microcosm method. It permits the study of basic principles in types of systems. Inferences can then be extended with suitable field studies to systems of larger size, more difficult to control. The ability to replicate ecosystems is a breakthrough for experimental ecology.

A sequence of P and R from a pond (Siler and Odum) is presented in Figure 2. That these pond systems resemble larger, natural systems is indicated by the similarity of their metabolism, the species that dominate the two, the ratio of number of species to individuals, and finally their efficiencies of photosynthesis in the two systems (one agitated by a motor and one by wind and tide).

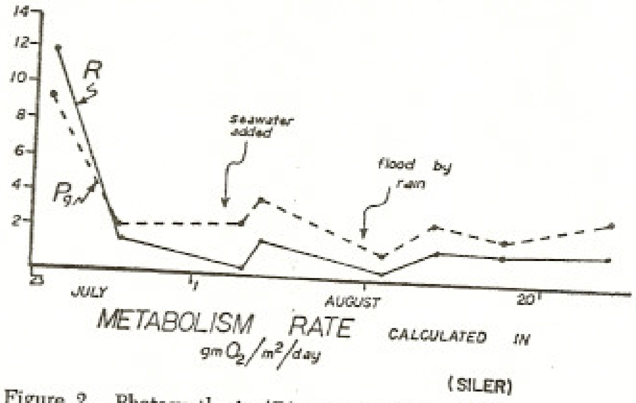

Figure 2. Photosynthesis (P) and respiration (R) in one sequence of stabilization of the oyster reef system. Data were taken by Walter Siler in 1960 in a plastic prototype of the unit in Fig. 1.

The General Case

The carbon metabolism of the oyster reef, Figure 4c, is only a special case of the general 4a, where 4c is created by the lack of flux save light and mechanical energy. In general, if one establishes the fluxes in and out, provides an evolutionary pattern by seeding and allows time to pass, a relatively rapid succession and a stable equilibrium follow. Let us use the old term climax to mean any open steady state with its stable structure and function.

Then we can classify the climax and succession in terms of P, R, and fluxes. Thus the city, 4b, is an extreme consumer with both biological and physical work accomplished by inflowing food and fuel. The oyster reef is the balanced 4c with no food or fuel being imported or exported. Finally, the Connecticut forest of the past is the productive 4d with wood as an export.

The four ecosystem types are again represented in Figure 3. Here the biochemical are separated from the heat engines. TΔX indicates fluxes of energy content from the system that are an inherent part of the process even under the theoretical condition of thermodynamic re-

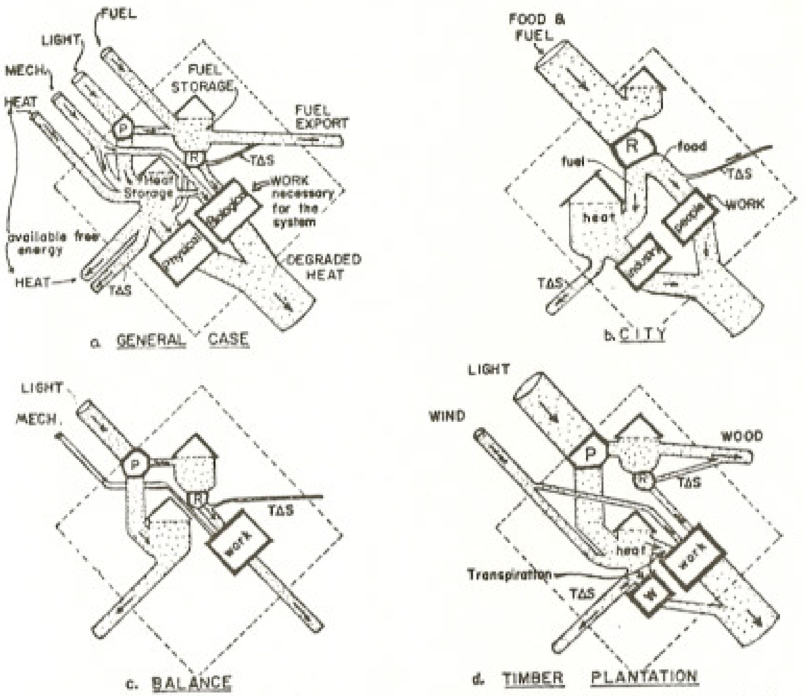

Figure 3. Generalized energy diagrams. *a.* General case with many of the major flows of energy of most ecosystems shown; *b.* a city with predominant basis of industrial fuels and human food flux; *c.* a balanced system in which photosynthesis and respiration are similar; *d.* a timber plantation representative of photosynthetic ecosystems that have net yields of stored energy in the form of exported organic matter. The W indicates physical work.

versibility when no energy is available for work. For example the heat of vaporization of transpired water leaves the system without being available for other work.

In such abstract matters, the land community differs not at all from the aquatic system. Because of the difficulties of technique our knowledge of land ecosystems with respect to P, R, and fluxes is less crystallized. Since this Conference concerns the suburban forest, perhaps it is useful to show some attempts to make the necessary P and R measurements on a forest system, even though the techniques are still imperfect.

The Montane Rain Forest of Puerto Rico

Over the past 5 years with the help of the Rockefeller Foundation and the cooperation of Dr. Frank Wadsworth of the U. S. Tropical Forest Station, we have attempted to estimate the biomass and metabolism of

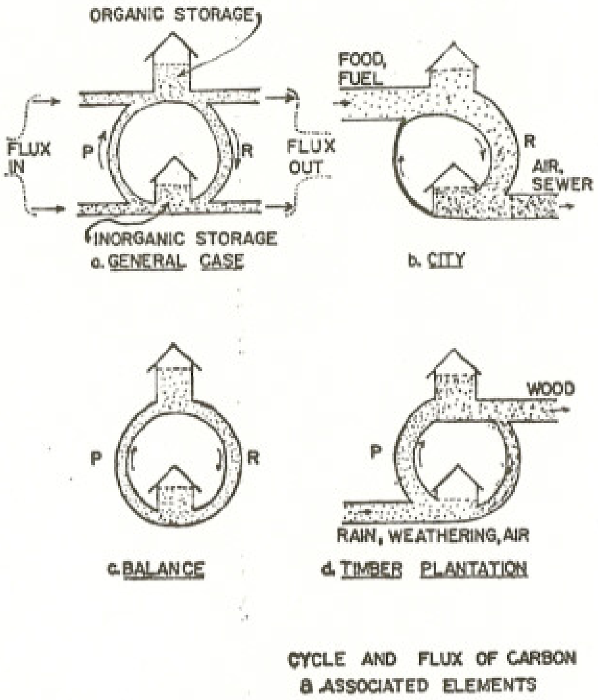

Figure 4. Generalized diagrams for the flux of matter associated with carbon metabolism. *a.* General case with four main fluxes; *b.* a city with predominant inflow of organic carbon and outflow of inorganic carbon dioxide and related inorganic wastes; *c.* balanced system with no fluxes of matter and with photosynthesis (P) equal to total respiration (R); *d.* a timber plantation, agriculture, or cultivated lawn with net yields balanced by influx of carbon dioxide and fertilizer (in rain or artificially added).

some main forest components of the lower Montane rain forest of Puerto Rico east of El Yunque. The approach is logically simple: (1) measure the gm^{-2} of leaves, animals, small roots, and other main metabolic components; (2) measure the photosynthesis and respiration per gram of the separate components with an infrared CO_2 analyzer in gas flow systems in the field; and (3) multiply the gm^{-2} times the metabolic estimates per gram to estimate total P and R of the system. Estimates for a patch of red mangroves at La Parquerra were recently published (Golley, Odum, and Wilson, 1962). Putting a large 70-foot bell jar over part of the forest and installing powerful air recirculation and refrigeration along with louvres for admission of rain may be a better method, but such expensive engineering has so far been beyond available resources.

The detailed studies of environment, biomass, and metabolism of the components of the forest are unpublished (H. T. Odum, W. Abbott, R. Selander, F. Golley, and R. Wilson, unpublished mss.) and final summation of metabolism of the parts apparently will require massive cutting of large plots of the forest for total leaf weights. Already, however, we can present a preliminary calculation based on assumed leaf quantity. Because the computations indicate magnitudes of metabolism and chlorophyll in the range of other systems measured, the order of magnitude may be correct. We hope that the preliminary calculation that follows will outline the need to measure total ecosystem functions in large forest ecosystems. We hope the data will reveal the feasibility and value of the forest "bell jar" project.

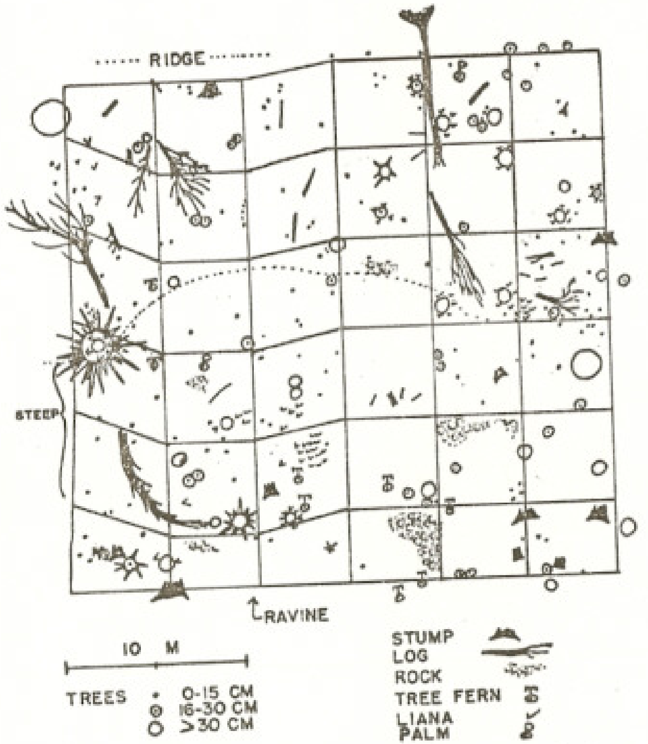

Figure 5. Quadrat with string grid used for preliminary computations on a patch of rain forest (see Tables 1 and 2).

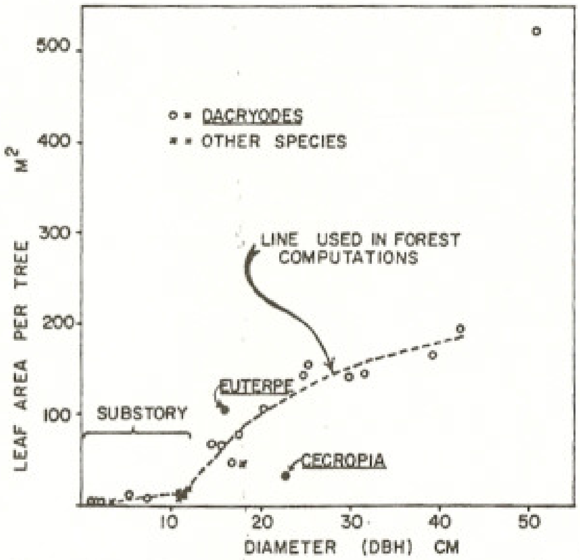

Figure 6. Leaf area as a function of trunk diameter for some trees in the lower Montane forest.

On a typical steep ridge in the Montane Forest, 36 quadrats were laid out with string (Figure 5). The principal trees were drawn in by size class: lianas, palms, tree ferns, and bromeliads were also counted. Chlorophyll A per area of representative leaves was measured (Odum, McConnell, and Abbott, 1958). Photosynthesis and respiration per area of leaf was measured in the field (Golley, Odum, and Abbott, 1962). Leaf area was related to tree diameter for one of the common dominant tree species *Dacryodes excelsa* (Figure 6). From Figure 6 we estimated the leaf area of 10 of the broad-leaved dominants, 29 medium-sized trees, and 132 small trees (Table 1). In other words, for this preliminary computation it was assumed that *Dacryodes* had a reasonably representative ratio of leaf area to trunk diameter. Then amounts of leaves were determined from the size classes. From leaf areas thus estimated, chlorophyll A and metabolisms were computed (Table 1). Details of the calculation are in the footnotes.

Estimates of soil respiration, respiration of animals, and leaf metabolism, Table 2, were taken from the manuscript cited above. The role of animals in metabolism was small.

If the preliminary calculations for the patch of Montane rain forest were correct, the following comparisons would be made with other ecosystems. The resulting area index (Table 1) of 7 m^2 leaf per m^2 ground would be two or three times that of the usual agricultural system. On the other hand, Varischi (1951) found 2.0 in a Montane tropical

TABLE 1. Leaf area, chlorophyll A, leaf biomass, photosynthesis, and respiration computed for principal components of a 900 m² quadrat of the lower Montane rain forest. Data from Chap. I-1 an ~~unpublished manuscript: H. T.~~ Odum, W. Abbott, ~~R. Selander, F. Golley, and R. Wilson~~. (from Odum, 1962). ~~Studies on the Productivity of the Lower~~ Montane ~~Rain Forest of Puerto Rico, Part 1.~~

	1[a] Leaf area m²/m²	2[b] Chlorophyll per forest area in January gm/m²	3[c] Dry leaf biomass per leaf area gm/m²	4[d] Dry leaf biomass per area of forest gm/m²	5[e] Night respiration gm/m²/12 hr	6[f] Net daytime photosynthesis on a sunny day gm/m²/12 hr	7[g] Gross photosynthesis on a sunny day gm/m²/12 hr	8[h] Net daytime photosynthesis on a rainy day gm/m²/12 hr	9[i] Gross photosynthesis on a rainy day gm/m²/12 hr	10[j] Total respiration per day gm/m²/24 hr
DOMINANT CROWN TREES										
10 Broad-leaved dominants (*Dacryodes* and others) greater than 25 cm DBH. *For special data and bases for computation see footnote k.*	1.67	0.64	227	380	0.54	3.02	3.56	2.50	3.04	1.08
3 *Cecropia peltata*[l]	0.05	0.019	203	10	0.024	0.23	0.25	0.076	0.10	0.05
3 Palms (*Euterpe globosa*)[m]	0.34	0.22	208	70	0.08	0.46	0.54	0.20	0.28	0.16
INTERMEDIATE TREES										
29 Medium-sized trees 15 to 25 cm DBH[n]	3.23	1.25	227	734	1.83	5.68	7.51	3.58	5.41	3.66
8 Tree ferns (*Cyathea*)[o]	0.06	0.016	117	7	0.011	0.07	0.08	0.007	0.018	0.02
132 Small trees 2 to 15 cm DBH[p]	0.95	0.22	155	147	0.74	1.61	2.35	0.76	1.50	1.48
27 BROMELIADS[q]	0.01	0.0009	38	0.5	0.0067	0.0036	0.0103	0.002	0.009	0.0134
GROUND HERBS AND SEEDLINGS[r]	1.03	0.30	41	41	1.27	1.07	2.34	0.62	1.89	2.54
TOTALS FOR LEAVES	7.34	2.67	......	1390	4.50	12.14	16.64	7.745	12.25	9.00

[a] Leaf area was obtained for trees from Fig. 6. The ratio of area of leaves to area of forest is sometimes called the leaf area index.

[b] Chlorophyll A values per leaf area were multiplied by values in preceding column 1. Values of gm/m² chlorophyll found were: broad-leaved crown trees, 0.42; *Cecropia*, 0.37; palm, 0.61; medium trees based on shade *Dacryodes*, 0.38; small trees based on mean of 14, 0.23; *Cyathea*, 0.27; bromeliads, 0.09; ground herbs and seedlings, 0.29.

[c] Data from the manuscript cited in the Table caption.

[d] Product of values in columns 1 and 3.

[e] Product of values of area in column 1 and data on respiration per leaf from the manuscript cited.

[f] Product of values of net photosynthesis and leaf area in column 1.

[g] Sum of columns 5 and 6.

[h] Product of values of net photosynthesis and leaf area in column 1.

[i] Sum of columns 5 and 8.

[j] Values in column 5 multiplied by 2.

[k] 150 m² leaf area per tree computed from Fig. 6 for 30 cm DBH Crown (10-15m). Light regime on sunny day included: 2 hr, 2000 fc; 2 hr, 4000 fc; 2 hr, 6500 fc; 2 hr, 8500 fc; 4 hr, 10,000 fc. Photosynthesis was taken as 0.15 gm C/m² of leaf area/hr in 85 per cent of crown tree leaves within crown above 10 m, and 15 per cent in shade also as 0.15. Respiration was taken as 0.027 gm/m²/hr. Light regime on rainy days was: 2 hr, 200 fc; 2 hr, 500 fc; 2 hr, 1500 fc; 2 hr, 2200 fc; 4 hr, 2700 fc.

[l] 0.13 m² per leaf; 314 leaves per quadrat; light regime as in footnote k; photosynthesis rate as in the manuscript, respiration 0.040 gm/m²/hr (mean of 4 determinations).

[m] 101 m² leaf/tree (Fig. 6). Light regime as in footnote k. Photosynthesis at 8500 fc, 0.12 gm/m²/hr; respiration, 0.01 gm/m²/hr.

[n] 100 m² leaf per tree for 20 cm DBH. Half was computed as crown leaves above 10 m as in footnote k; half was computed as in shade leaves in footnote p. Light regime: 10 hrs above 580 fc, 2 hr at 300 fc, and photosynthesis, 0.10 gm/m²/hr. Respiration of shade leaves 0.065 gm/m²/hr; respiration of crown leaves, 0.027 gm/m²/hr.

[o] 0.1 gm/m²/hr; respiration, 0.015 gm/m²/hr; net photosynthesis on rainy day, 0.010 gm/m²/hr at 200 fc.

[p] 6.5 m² leaf area per small shade tree (mean of 10 trees: 3.4, 10.5, 17.5, 10.1, 9.0, 9.8, 2.1, 0.7, 0.94, 0.70). All leaves of small trees were computed as shaded; light in the shade on a sunny day: 14 hr, above 500 fc, with photosynthesis 0.15 gm/m²/hr; 2 hr at 400 fc and 0.10 gm/m²/hr. Respiration of shade leaves, 0.065 gm/m²/hr; respiration of crown leaves, 0.037 gm/m²/hr.

[q] 0.40 m² leaf per bromeliad; photosynthesis 0.010 gm/bromeliad/hr; respiration, 0.0093 gm/individual/hr.

[r] Leaves were picked from quadrats and dried. 82 gm/m² leaf biomass on open canopied ridge; 0 in ravine; mean 41 gm/m² of forest; 40 gm/m² of leaf area. Photosynthesis in shade, mean of 13 herbs and seedlings, 0.087 gm/m²/hr; respiration, mean of 7 determinations, 0.105 gm/m²/hr.

TABLE 2. Some overall metabolic estimates for a plot of lower Montane rain forest[a]

P, TOTAL GROSS PHOTOSYNTHESIS (Table 1)		12-16 $gm/m^2/day$
R, TOTAL RESPIRATION		
Total leaf respiration (Table 1)	9.0	
Soil, litter, and root respiration[b]	5.8	
Animal respiration by 3.7 gm/m^2 animals (dry)	0.18	
Total[c]	15	→ 15 ←

[a] These include some unsubstantiated assumptions about leaf quantities as indicated in the text and in Table 1, column 1.

[b] Employing an infrared CO_2 analyzer in an open system beneath a shelter of foil, the metabolism of the natural forest floor surface was found to be a function of the rate of air flow across the litter. From ammonium chloride smoke measurements in April, 1962, air velocities averaging 14 cm/sec. were found 2 cm above the litter. Under the disc or shelter of aluminum foil supported about 0.5 cm above the irregular litter surface, a velocity of 14 cm/sec occurred when air was drawn at about 30 liters/min. The respiration rate of the forest floor surface that was equivalent to this flow was about 0.24 $gm/m^2/hr$. This estimate is probably high since the natural air flow at 0.5 cm is likely less than that measured with smoke at 2 cm.

[c] Respiration of stems and trunks was not measured.

forest at Rancho Grande, Venezuela. The large difference between two estimates for Montane forest emphasizes the need for total leaf counts. The chlorophyll A of about 3 $gm\ m^{-2}$ is somewhat larger than the usual 0.5 to 2.0 $gm\ m^{-2}$ in land and water communities. The total gross photosynthesis of 14 to 20 $gm\ m^{-2}\ day^{-1}$ corresponds to an efficiency of about 10 per cent of the usable light reaching the forest and is in the range of the most productive systems so far measured: algal cultures, sewage ponds, the best agriculture, coral reefs, and underwater grass flats.

The preliminary calculations provide a possible solution to one question troubling Dr. Frank Wadsworth and associates, tropical foresters managing this forest. The growth rate of the trees measured over 20 years has been small, 0.05 to 0.12 inches per year. The dominant trees are several hundred years old. Is this slow growth due to lack of light, lack of nutrients, or inadequate photosynthesis for other reasons? The calculation of respiration as 9.0 $gm^2\ day^{-1}$ due to leaves and 5.8 due to the soil, root, and litter indicates very little production is left for any net growth with most of it being used to sustain leaf and soil activity. The apparent reason for slow growth is thus not any inhibition of gross photosynthesis, but the full development of the ecosystem structure requiring most of the production for respiratory maintenance. Such metabolic arrangements are not unexpected in a climax system where nutrients must be mainly recirculated. The forest could be manipulated to divert more of its production into products desirable by man whether timber or aesthetic aspects, but it is very unlikely that total output could be increased without adding auxiliary energy since the efficiency may already be as high as has ever been measured in other systems (if the leaf assumption is of the correct order). In other words, the Montane forest is more like Figure 4c than 4d.

The behavior of the Montane forest seems similar to the microcosms of balanced aquaria in the constant temperature rooms at the Institute of Marine Science where Beyers (1962) has done exhaustive studies on the intricate coupling of P and R, one complementing the other in the supply of nutrients. The coupling is so close that the ecosystem has a total metabolism independent of temperature even though the separate organisms have the usual responses to temperature. For 4 years, close coupling of P and R also was seen in the Texas Laguna Madre, an example of the general case (Figure 4a) (Odum and Wilson, 1962). The unity of aquatic and terrestrial systems provides a powerful, single ecological theory for predictions about unstudied systems like the Connecticut suburban forest. To maintain diversity both the climax Montane forest and the aesthetic forest channel energies similarly.

PRINCIPLES OF ECOLOGICAL ENGINEERING

Power Take-off From Civilization

There is a spectrum of energy budgets from systems in which power supplements by man are small to those in which the power subsidies are large. At one extreme are the completely natural forest or pond whose many processes run on such natural energy sources as the sun or inflowing organic matter. At the other extreme, where power subsidies from man dominate, are the environmental industries: agriculture, traditional forestry practices, and waste disposal engineering. Characteristic of technological progress in man's use of the natural environment has been the ever increasing ratio of subsidized power to the natural power supply. In the mechanized production of food, the power from gasoline may exceed that from sunlight. Knowledge of the natural ecological systems and the environmental industries has been growing, but relatively little is known of the potentialities in the zone where the power subsidies by man are small, but sufficient to keep the system within bounds. The suburban forest and the Texas Bays are of this type. Recognizing the shared energy sources from nature and from power take-off from civilization, we suggest the term ecological engineering for those cases in which the energy supplied by man is small relative to the natural sources, but sufficient to produce large effects in the resulting patterns and processes. Because man's aesthetic desires may be often related to properties of complex and climax systems and because these systems are more nearly self-maintaining and require relatively small power subsidy, the suburban forest will involve ecological engineering.

Power take-off from civilization into a forest may take many forms such as: regular fertilizing, spraying, pruning of particular species, food subsidy for some animal, wildlife management, and seeding. Whereas we may have a good idea of the immediate result of one of these actions, we know relatively little about the long-range effect on the whole system. We know relatively little of its readjusted successional and steady states when the auxiliary energy supply is on a regular basis. Experimental plots with auxiliary power inputs on a regular basis can provide answers. Some idea of the sustained power requirements for significant changes should soon emerge.

Synthetic Systems and Domestication

Synthetic ecosystems include conditions and combinations of organisms never before in existence. Just as in the above example of an oyster reef pond where a new synthetic system was developed by combining previously existing species complexes (prototypes) with some new imposed conditions, so with man in the suburban forest a new synthetic system is being developed by combining the natural species complexes with some new imposed conditions such as interspersed houses and clearings. When multiple species seedings are done in artifical aquatic systems, a functional ecosystem soon evolves with species-number distributions like those in wholly natural systems (examples, Odum and Hoskin, 1957; Beyers, 1962). Presumably, similar processes will act in a synthetic system of multiple natural seedings plus the imposed habitations of man. In the terrestrial systems, however, dispersal and rapid introduction of multiple species may be retarded, especially the larger components. Multiple introductions from throughout the world may permit more diverse combinations to evolve, more closely integrating the habitation of man.

Domestication is a special development of synthetic systems through multiple importations and genetic adaptations. In domestication, few species have yet been fully adapted to such purely human systems as cities. However, in the semi-inhabited suburban forest, enough evolutionarily-old prototypes may remain for the existing species to develop in a reasonable time the diversity for stability. Eltonian population invasions need to be recognized as simplified preliminary phases in the early organization of new systems from preadapted components.

Past emphasis in research on physiology, horticulture, and husbandry of single species in systems involving man may not enable us to predict results where diversity, complexity, and self-sustaining complexes are needed without large energy subsidies. We need to know something about the nurture and manufacture of synthetic systems.

A fictional account of man's house as a synthetic, evolutionarily-young system was developed by Ordish (1960). In an interesting account of 500 years in the history of a house, he includes reasonable though fictional time graphs of populations of roaches, wood borers, humans, and other animals. He considers the rise and fall of the system including such sophisticated considerations as relative metabolic energies of the human and other dwellers. He considers the invasion and domestication of species new to the human system. In the crudeness of data so far available, ecosystem science may be no less fictional, and the approach is identical. In drawing together a substantial bibliography on the human house and in providing a broad-brush plan for its study, the book, however intended, is a contribution to the methodology of quantitative ecology, and perhaps a guide to the studies needed for the system of man and the suburban forest.

A different approach was used by Odum, Muehlberg, and Kemp (1959) and by Arvid Anderson (1960) in considering man as part of the Texas bay system, using dollar-per-acre equivalents to compare cultural and biological metabolism.

Arresting a Successional Stage Into a Climax

If a successional stage is developing towards a steady state by accumulation of some quantity such as organic matter or nutrients bound in soil systems, one may arrest the successional stage and hold the system in a new steady state by introducing a new flux that removes the organic matter or nutrients.

Ecosystems have been manipulated in this way in sewage algal systems by Oswald where, by control of rate of flux, the populations were maintained in various climax adjustments comparable to successional stages from 1 to 14 days old. The principle is well known in fire management. Acknowledging the abstract flux idea underlying the old practice may aid in developing new procedures for new systems. Similar influxes may essentially change the type of ecosystem. For example, by changing the fluxes of organic matter and water through the spraying of wastes into a forest, Little, Lull, and Remson (1959), produced a mesic herbaceous system instead of the normal forest system in New Jersey.

Abbreviating Succession

Where succession involves accumulation or consumption of quantities between starting and final climax, the successional stages may be abbreviated by artificial addition or removal of that quantity. If the critical quantity is an inorganic elemental substance, such manipulation may be especially practical once the nature of the quantities controlling these transient states is known.

ECOLOGICAL DETERMINISM

Progress and the Balance of P and R

Here in New Haven where Ellsworth Huntington wrote on a geographical determinism, it may not be courteous to discuss ecological mechanisms determining early civilizations of man, since Huntington's proposed influences were physiological rather than ecological and so naive that a generation of sociologists was repelled.

Nonetheless, full activity by men obviously depends on a full flux of energy, and one may consider the patterns of energy availability in time and space as major causal agents in the cultural evolution of man. In times prior to the era of fossil fuels, man's supplies of energy were obtained immediately from photosynthetic products of the land: timber and foods. Productivities of plants and their dependent animals were highest in communities with unlimited raw materials for photosynthesis. This happened along the boundaries of land and water and especially where mechanical energy of water along rivers, reefs, and shores concentrated raw materials and foods for organic growth. The high yields of energy from such environments may have been the essential reason for human colonization in such places rather than communication, transportation, or direct use of water. High productivity of the environment was an essential but not a sufficient condition, for the energy flows of many highly organized ecosystems are large but so branched that little energy is available at any one spot or time for one large species in competition with hundreds of specialized types.

In ecosystem terminology, man could flourish to the extent that P (photosynthesis) was not only large but in excess of R (respiration). In situations where R was balanced with P, organic matter was used as fast as it was produced by the metabolism of the biotic community and little was available for man. We may speculate on the metabolic types of natural ecosystems most amenable to man as he emerged from some restricted animal niche.

Is progress and human culture possible in either primitive or oil ages only when energy beyond subsistence becomes available? In the pre-fossil fuel eras extra energy became available in nature only when photosynthesis exceeded the respirations of the ecosystem *in situ* or when P and R became separated either in time or in space and organic matter accumulated temporarily. The balance of ecosystem processes is the metabolic basis for ecological determinism based on energy budgets.

P exceeded R with temporary storage excesses in the temperate and higher latitudes where the seasons were keeping the processes out of phase. Accumulations of animal biomass for a hunting economy were possible in such oscillating systems. Tropical areas with dry and wet seasons may similarly have had peaks in P and R separated in time and hence had temporary food accumulations. Areas with net growth also occurred in succession when fire, clearing, or flood reduced matter and a recovery scheme of P greater than R followed. Early cultural progress in semi-arid and temperate areas; along temperate water, seashores, and rivers; in areas with seasonal energy pulses; in monsoon areas; in savanna belts of Africa; and in the dry-wet seasons of middle America are not inconsistent. Wherever extra energy was available momentarily, culture and progress flamed, new know-how for getting a larger part of the energy emerged and was absorbed into the cultural memory. Thus the evolution was one of widening energy input paid for by the energy expenditure during surplus periods.

Then man's role began to increase as a larger fraction of energy was taken, but the opportunity from system failure due to actions of man also began to increase as his role became greater. Progress spread, and cultural developments of primitive man beyond status quo and subsistence were nurtured where P was already in excess of R or in other localized areas of organic matter accumulation.

Many things about this early development of man may make energetic sense when the distribution of P and R are considered. The development of primitive agriculture with power take-off from the photosynthetic system via domestic animals is in the anthropological record. Did small shifts in climactic belts transform the seasonal dry-wet forest of the Mayans into more of a steady state rain forest with vast decreases in P/R ratio and available energy for man?

Only in the 19th century did new energy sources become available beyond the immediate photosynthetic process; only recently was the P and R basis of survival superceded. With cultural survival so recently on a new basis, are man's instinctive attitudes to nature mainly inappropriate but lingering to be reckoned with in the Connecticut suburban forest and the fishing waters of Texas?

Two Extremes in Man's Ecological History

Man's cultural development is thus directly related to the energy budget available in excess of his previous level of sustenance. Where he was adapted like the pigmy to the heavy non-seasonal forest, he adjusted like the pigmy to a small percent of the total metabolism taken regularly from a system of great stability but with little excess for progress and the future. In a stable climax ecosystem such as a coral atoll or a Darien rain forest man was maintained by the system, but with relatively little net growth; there was little opportunity for the human population once at its equilibrium to gain surplus energy for new purposes. Thus in the stable climax, man may have been stable but unable to innovate. Only a tiny percentage of the human populations could spend time in activity other than subsistence. Here man was fully at the mercy of the system of which we was a part. Perhaps fortunately for him, he controlled only a small proportion of the total energy of the system. The long evolution of the natural systems had provided some stability as his reservoir of protection.

Where man inhabited the variable ecosystems, energetics were different. There were wide variations and temporary energy excesses and with the temporary excesses invested in progress his culture blossomed and died like the desert flowers. When man converted a primitive hunting system to an agricultural system, the carrying capacity was increased. His new available energy sources were those products of forests or fields that he could divert from other consumers that would otherwise have eventually respired the organic matter. Control was easiest for him in fluctuating ecosystems where instability had prevented the tight organization of branching food chains of biotic specialists to preclude collectively his access to the energy flux.

Many aspects of the early history of man are understandable in terms of the irregular pulsing of energy for progress. The development of nomad and military mechanisms of adapting to irregular energy flows gained control of the system's energy flows. The more rapid cultural developments in the Near East and Asia are consistent with the wider variations in the pulsing of ecosystem energy availabilities. The rich but irregular cultures of the monsoon belts and subtropics are of P and R imbalance.

Ecological Roots of the Aesthetic

Deep within man's physical and cultural inheritances are environmental preferences that create strong desires even in modern times, as in the Connecticut suburban forest or the Texas Lagunas. One may speculate about instinctive drives and their possible significance for survival in the former eras when man's energy supplies were ecologically different.

To some extent these feelings now seem contradictory, for some seem to relate man to the stable climax and some to relate man to successional, aperiodic, and oscillating systems. It may well be that the relict instincts of man would place him on the forest edge between the successional plot and the climax, on shores for their high productivity, and in places where several kinds of productivity may be tapped.

What are some of man's preferences that seem related to climax?

Love of diversity, color in animals, multiple flowers, complex bird songs, mesic atmosphere, green softness, mossy-covered forest floors, shade?

What are some of man's preferences that seem related to successional stages? Love of a panoramic view, forest borders, and sunny spots, masses of homogenous herbs like the bluebonnets of the Texas sage. Whence come his likes? Are they completely unrelated to early survival? Are they related to survival as a part of a stable system, or are his likes tied to the momentary high pulsing of some less permanent system?

Whatever may be the functional roots of his inheritance of aesthetic preference, the excess energy of cultures rich in energy are soon diverted from survival into the satisfactions of the aesthetic preference whether they are still related to survival or not. Well-developed love of Nature, like other more formal arts, is an indicator of a high ratio of energy influx to subsistence energy demand.

If the aesthetic needs of man were formed in the past and nourished in relation to the hard realities of energy budgets, it is a reciprocal corollary that a system retaining the wrong aesthetics in diversion of its energetics may be eliminated in competition as in the ages past. Are the ecosystems like the suburban forest to be managed according to relict aesthetics related to the positions of tribal lodges or according to new aesthetics yet to be evolved according to new energy bases? Dare we manage the forest for the objective of a former aesthetic system when it may be non-essential and diverting energy needed for making gains for survival? Will competitive political and cultural systems roll over a society managing its modern ecosystems according to its tribal lores?

How sure are we of the continuance of the new energy sources? Are the precious decades of excess fossil energy now available for progress part of a receding flame? Should we manage our planning for survival in a P and R system that will prevail again? Should the forests and the bays be studied for maximum energy output for man at a later time? If man is again to be on a photosynthetic basis, the forests and bays might best be prepared for management no longer unsubsidized by present power feedbacks from the fuel-rich industrial complex.

Is it possible that non-functional aesthetic systems serve as energy buffers? Survival of a system may require the availability of great power reserves for short, violent periods of competition, disaster, and fluctuations of conditions. A system which builds its populations and reproduces its basic functional units to the maximum carrying capacity, like overcrowded grain beetles, has no power reserves. Is it possible that the persistence of the arts and the aesthetics in the human system serve to bleed off enough energy during ordinary times to prevent its preemption for maintenance so that during system stress, this power drain can be immediately tapped into the main survival functions that may be unexpectedly critical?

With some humor, the artist, the Connecticut woodland pruner, and the Texas sea trout fisherman can imagine their energetic role as the vital protector of power reserves. No doubt, however, there is some proper percentage of the total budget for the artist's power flywheel.

Apparently, therefore, there are three main possibilities:

1. Management according to man's present aesthetics with the values and risks of diverting energy.
2. Management towards a time of declining subsidies of non-solar energy with study and forest system planning for timber and agricultural use once again.
3. Management according to man's present power systems with aesthetics retuned and controlled by the imagined realities of survival.

If we knew which of these or other objectives should dominate our energy planning, we could readily indicate the basic energetic boundary conditions to be used in ecological synthesis and engineering. Apparently, the momentary facts of economic life in forested Connecticut as along the Texas Gulf coast are demanding management for existing aesthetics.

SUMMARY

Using theoretical diagrams and the oyster reef pond ecosystem as an example, the methodology of studying and manipulating the gross photosynthesis and total respiration of ecosystems was outlined with techniques of ecological engineering: multiple seeding, self stabilization, replication by intermixing, energetic subsidization with power from man's civilization, and regulation by flux control.

To indicate the methodology as applied to a forest system, preliminary calculations were made of total photosynthesis and respiration of a patch of lower Montane rain forest of Puerto Rico. The slow growth of tree trunks was attributed to large respiration of leaves and forest floor rather than to any limitations of initial photosynthesis. Thus some approaches to management were indicated from metabolic considerations.

A theory of ecological determination involving the distribution of P and R in space and time was discussed in relation to man's early cultural role within ecosystems including two extremes, one with man as a minor component of complex, climax, and stable systems of long evolutionary history; the other with man the dominant consumer in erratic, successional, wildly fluctuating and unstable systems with temporary energy excesses to pay for progress. The possible ecological roots of his aesthetics in these systems were discussed and questions raised about their role in emerging new systems with shifting energy bases.

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Participants in the Lockwood Conference. Left to right: H. T. Odum, H. J. Lutz, F. W. Went, F. F. Darling, Marston Bates, S. H. Spurr, J. D. Ovington, Peter Farb, Pierre Dansereau, and M. B. Russell.

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