



TIME'S SPEED REGULATOR: THE OPTIMUM EFFICIENCY FOR MAXIMUM POWER OUTPUT IN PHYSICAL AND BIOLOGICAL SYSTEMS

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AMONG THOSE who deal with the many separate sciences, and among those who seek universals common to the various sciences, there is a search to find out why the thousands of known processes are regulated, each one at a characteristic rate. A common denominator has been found in the concept of entropy which permits the comparative study of energy changes. For closed systems natural spontaneous processes are directed toward an entropy increase, so that entropy has been appropriately called "time's arrow."

What has been lacking, however, is a generalization applicable to open systems which would indicate the *rate* of entropy increase. The Second Law of Thermodynamics does not indicate the magnitudes of the rates or explain how open systems are adjusted. If it exists, we need to discover "time's speed regulator." Theories of rate processes are available for simple molecular scale systems, based largely on statistical thermodynamics, but such detailed pictures are impractical in complex systems. In the theory of automatic controls (servo-mechanisms), in economics, and in other fields, another approach may be used involving the assumption that rates in question are proportional to the forces causing them. In order to understand rate adjustments in living systems, additional hypotheses are required.

In this discussion a simple general expression for idealized systems is presented relating efficiency and power. Our proposition is that natural systems tend to operate at that efficiency which produces a maximum power output. With expressions derived from this basic assumption, it is possible to distinguish between the maximum power hypothesis and alternative propositions, e.g. the supposition often made that systems tend to run at maximum efficiency.

One of the vivid realities of the natural world is that living and also man-made processes do not operate at the highest efficiencies that might be expected of them. Living organisms, gasoline engines, ecological communities, civilizations, and storage battery chargers are examples. In natural systems, there is a general tendency to sacrifice efficiency for more power output. Man's own struggle for power is reflected in the machines he builds. In our energy-rich culture, most of our engines are designed to give maximum power output for their size.

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Utilizing ideas derived earlier, Lotka (1922) proposed a "law of maximum energy" for biological systems. He reasoned that what was most important to the survival of an organism was a large energetic output in the form of growth, reproduction, and maintenance. Organisms with a high output relative to their size should win out in the competitive struggle for existence. Let us make the following postulate: Under the appropriate conditions, maximum power output is the criterion for the survival of many kinds of systems, both living and non-living. In other words, we are taking "survival of the fittest" to mean persistence of those forms which can command the greatest useful energy per unit time (power output). Holmes (1948) discusses the historically independent postulates such as that mentioned above which attempt to predict general trends for open systems. Although there are probably many situations where power output is not at a premium, let us in this discussion consider that type of energetic coupling which does produce a maximum power output.

A simple process involving an energy transfer can be considered as a combination of two parts. In one direction, there is a release of stored energy, a decrease in free energy, and the creation of entropy. In the other direction, there is the storing of energy, the increase of free energy, and an entropy decrease. The whole process consists of a coupling of the input and output. The Second Law of Thermodynamics requires only that the entropy change for this "open" system and its surroundings be a simple increase in order for the over-all process to occur. It is possible for the input and output to be coupled in various ways so as to produce varying rates and efficiencies.

We shall consider below the energy transfer in a particular class of open systems. The potential of the energy available to these systems will be regarded as fixed, as well as their size and certain other characteristics. However, the coupling arrangements will be considered as variable. Having indicated above why maximum power output may be important, our proposition is that *these systems perform at an optimum efficiency for maximum power output, which is always less than the maximum efficiency.* In fact, it will be found that in order to operate at maximum power, the efficiency may never exceed 50 per cent of the ideal "reversible" efficiency. This sort of behavior has been noted before in many separate scientific fields.

Simple Example—Atwood's Machine

Before considering the general case let us examine the Atwood's machine pictured in Figure 1. The falling of weight M_1 converts potential energy into kinetic energy and then into wasted heat as the weight strikes the basket. The elevation of weight M_2 is the part of the process involving energy storage. Weights M_1 and M_2 are coupled by the string and

pulley. The average rate at which M_1 falls gives the power input, whereas the average rate at which M_2 rises gives the power output. The weight M_1 is kept constant, but the weight M_2 is varied. The ratio of the two weights M_2/M_1 is the efficiency.



FIG. 1. Atwood's Machine. The power input due to the falling weight M_1 drives the elevation of weight M_2 which stores potential energy.

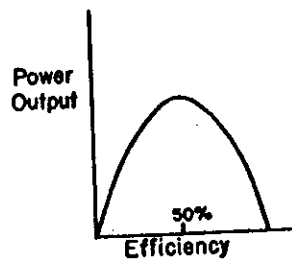


FIG. 2. Power output is given as a function of efficiency for systems where there is no leakage (l) and the efficiency (E) is thus equal to the force ratio (R).

If the weights are nearly the same there is almost no velocity of movement and the power output approaches zero as the efficiency, M_2/M_1 , approaches 100 per cent. At the other extreme with weight M_2 at zero, weight M_1 falls at a maximum rate with a zero efficiency, so that again the power output is zero although the power input is at the maximum. Between these extreme positions there is an optimum ratio of M_2/M_1 which produces a moderately high velocity with a moderately large weight lifted. As one can demonstrate in a physics laboratory, the optimum arrangement for maximum power output is at 50 per cent efficiency (Fig. 2). A larger M_1 permits proportionately larger power input and power output, but does not change the shape of the curve.

The Atwood's machine can be considered as in an open steady state condition only by thinking of successive identical weight drops with an average velocity. This example was presented first in order to make the central idea clear. Atwood's machine differs from the general case in several ways: (a) the two coupled processes are of the same type; (b) the two flow rates are the same since the weights were directly coupled with a string; (c) repair and replacement were not considered.

General Power-Efficiency Equation

Some fairly recent extensions of the theory of thermodynamics of open systems permit us to associate power output and efficiency in a general way. The derivation is based on concepts developed by Prigo-

gine, Onsager, de Donder, and others, and the methods have been well summarized by Denbigh (1951) and de Groot (1951).

Any intensive property of a system, such as a voltage, food concentration, pressure difference, surface tension, temperature gradient, concentration gradient, etc., may be regarded as a thermodynamic force (X). Coupled with each force is a generalized flux (J), such as electrical current, growth rate, rate of extension of volume or area, flow of heat, etc. In the system used here it is customary to choose these quantities so that the products JX have the dimensions of power. We will deal only with the simple case of two forces and two fluxes, which will be related to the input and output of power in our system. These must be so chosen that the following relation is valid:

$$T dS/dt = J_1 X_1 + J_2 X_2 \quad (1)$$

where dS/dt is the rate of increase of entropy of the system and its surroundings, and T is the absolute temperature. J_1 is the flux into the system under the influence of force X_1 ; J_2 is the flux output associated with force X_2 . For simplicity, this output might be thought of as power stored for future use. In words, equation (1) says simply that the rate of dissipation of power is equal to the useful power input minus the useful power output. Next, it is to be noted that the forces X are related to fluxes J . It is usually assumed that the J 's are linearly related to the X 's. Suppose that our system is characterized by three constants, l , f , and c . Their significance will be discussed below. Then we will set down:²

$$J_1 = (l + cf)X_1 - cJX_2 \quad (2)$$

$$J_2 = -cJX_1 + cX_2 \quad (3)$$

It is important to note that cf , the coefficient of X_2 in the equation for J_1 is the same as the coefficient of X_1 in the equation for J_2 . In effect, one of four quantities required to describe the system has been eliminated. The identity of these two coefficients is called the "Onsager reciprocity relation" which is based on the principle of microscopic reversibility.

The constants l , f , and c are defined as follows. First, suppose that the force X_2 is adjusted so that it balances the driving force, X_1 , and so that J_2 becomes zero since there is no output. Then

$$f = (X_2/X_1)_{J_2=0} \quad (4)$$

In the case that X_1 and X_2 are two different kinds of force, the factor f shows how they are related dimensionally.

Under this same condition, when there is no output of useful power, there may be a certain input flow of energy which we may call leakage.

² In the formal treatments, one usually writes $J_1 = L_{11}X_1 + L_{12}X_2$ and $J_2 = L_{21}X_1 + L_{22}X_2$, along with $L_{21} = L_{12}$. The L 's are called "phenomenological coefficients." They are then related to some physically measurable quantities of the system. These steps are omitted here to shorten the derivation.

In a thermocouple there is a certain irreversible flow of heat when the voltage of the couple is balanced by an external potentiometer (Fig. 6):

$$J_{1(x_1 - \theta)} = lX_1 \quad (5)$$

When there is no driving force X_1 and a force X_2 is artificially applied to the system, there is a certain flow J_2 which is:

$$J_{2(x_1 - \theta)} = cX_2 \quad (6)$$

In the electrical case c is the electrical conductivity of the output process of the system.

Having defined l , f , and c , a word should be said about the limits of applicability. All that follows (and for that matter, the Onsager relation itself) depends on the assumption that the system is not far displaced from true thermodynamic equilibrium. Under that limitation, l , f , and c may be regarded as constant; where this assumption may not apply these equations may be used only as a first approximation.

We can now calculate the relationship between efficiency and power output. Before doing so, we shall define a certain parameter R , which is related to the ratio of the forces X :

$$R = X_2/fX_1 \quad (7)$$

It will be supposed that the desired operating level may be attained by varying R for the system. Note that R , the force ratio, is dimensionless, and takes on a series of values from zero to one. This makes possible the comparison of systems which differ greatly in type.

The useful power input will be taken as $P_1 = J_1X_1$ and the useful power output as $P_2 = -J_2X_2$, consistent with equation (1):³

$$P_2 = cf^2X_1^2R(1 - R) \quad (8)$$

It is readily shown by setting the derivative equal to zero that, for maximum power output, R must be set at $1/2$. This is an important result, for it shows that for any coupled process which operates on these general principles, maximum output is obtained when the ratio of the thermodynamic forces (after conversion to common units) is equal to $1/2$. As shown in Figure 1, for machines of the class under consideration

$$P_{2(\max)} = \frac{cf^2X_1^2}{4} \quad (9)$$

The efficiency for conversion of useful input power is $E = P_2/P_1$ or:

$$E = \frac{R}{1 + l/cf^2(1 - R)} \quad (10)$$

³ For cases involving heat flow, X_1 is proportional to the temperature difference, ΔT . It is common practice to choose J_1 itself equal to the heat flow (Q). Then X_1 automatically becomes $\Delta T/T$, and $J_1X_1 = Q\Delta T/T$ is indeed the useful power input. The efficiencies of useful power conversion which we calculate below for heat conversion cases do not include the Carnot efficiency, for this has already been taken into account.

The relationship of efficiency, E , to force ratio, R , is represented in Figure 3, which shows how E depends on the operating level R .

At the level of maximum power output,

$$E_{(P_2 \text{ max})} = \frac{1}{2(1 + 2l/cf^2)} \quad (11)$$

Note that regardless of the value of l , c , and f , E at $P_{2 \text{ max}}$ may never exceed 50 per cent. Also, there may be natural limitations on the ratio l/cf^2 which will become apparent later.

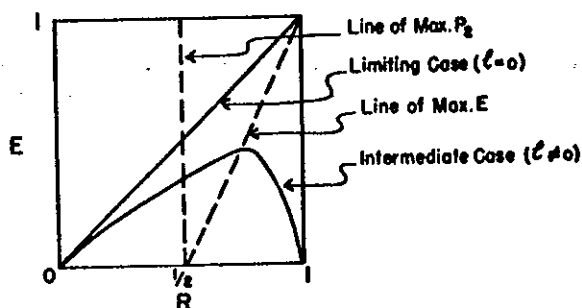


FIG. 3. Relationship of efficiency (E) and force ratio (R). A typical curve is drawn for the case where leakage (l) is not zero. E values for maximum power output are located on the vertical dashed line where R is $1/2$. Maximum efficiency and associated R values are found on the slanting dashed line.

In order to operate at maximum efficiency, the conditions chosen must be quite different. Let the value of R which will result in the highest efficiency be R^* . Then

$$E_{(\text{max})} = 2R^* - 1 \quad (12)$$

where R^* is equal to

$$1 - \frac{l}{cf^2} (\sqrt{1 + cf^2/l} - 1)$$

This value may be substituted in equation (8) in order to find the power at maximum efficiency.

In the case of heat flow, the over-all efficiency is $E_{(\text{total})} = E\Delta T/T = P_2\Delta T/P_1T$ as noted before. This relation holds because we have chosen to define our efficiency (E) in terms of the ratio of the useful power output to the useful power input.

Having related power and efficiency for the general case, let us consider some varied applications.

Examples from Various Types of Phenomena

In the paragraphs below some physical, biochemical, biological, ecological, and social systems are given to which the optimum efficiency

for maximum power analysis can be applied. In each case part of the system is described as the driving process and part as the driven. A schematic diagram of the coupling action of each system is shown in Figures 1 to 12. Some of the systems such as the Atwood's machine and electric cells which are coupled are symmetrical. Leakage (lX_1) is the power dissipation that occurs even when the output flow (J_2) is stopped due to a balance of forces X_2 and X_1 .

Two of the cases include self-replacement. Actually no system is in a truly steady state unless it includes self-reproduction to balance inherent wear. Efficiencies as customarily considered in simple systems omit replacement which is required if the system is self-repairing. Efficiencies computed to include self-repair are of course lower than those which do not include replacement costs. Repair in the example of an animal digesting and concentrating food is the basal metabolism and thus was included as leakage.

The physical systems described below are mostly self-explanatory. Some further comment on biological systems follows:

GENERAL CASE

J_1 —input flux; X_1 —"force" driving J_1 . J_1 and X_1 refer to the exergonic driving process. J_2 —output flux; X_2 —"force" associated with J_2 . J_2 and X_2 refer to the endergonic driven process. f —factor of proportionality relating X_2 and X_1 ; c —conductivity giving the value of J_2 when X_1 is zero; l —leakage giving the value of J_2 when $X_2 = fX_1$ and J_2 is zero.

ATWOOD'S MACHINE (Fig. 1)

J_1 —average velocity of fall; X_1 —force of gravity on weight M_1 . J_2 —same as J_1 ; X_2 —force of gravity on weight M_2 . l —zero; c —average rate of rise per unit weight of M_2 ; f —unity.

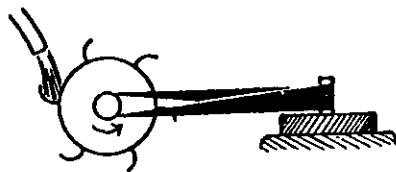


FIG. 4. Water wheel driving a grindstone.

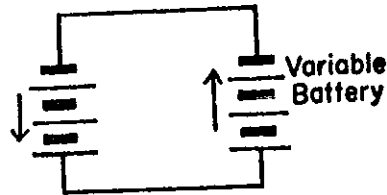


FIG. 5. One battery charging another battery.

WATER WHEEL TURNING A GRINDSTONE (FIG. 4)

J_1 —rate of water flow; X_1 —potential energy drop per unit of water flow. J_2 —angular velocity of grindstone, taken in direction opposite usual motion. X_2 —frictional torque opposing motion of grindstone.

l —zero except for a wheel with leaky buckets; c —inversely proportional to rotary friction other than in grindstone itself; f —related to gear ratio between water wheel and grindstone.

ONE BATTERY CHARGING ANOTHER BATTERY (FIG. 5)

J_1 and J_2 electric current; X_1 voltage of charging battery. X_2 —voltage of battery being charged. l —related to the shelf life, or self-discharge of the batteries; c —electrical conductivity of the circuit; f —unity.

THERMOCOUPLE RUNNING AN ELECTRIC MOTOR (FIG. 6)

J_1 —heat flux; $X_1 = \Delta T/T$ where T is the absolute temperature. J_2 —electric current; X_2 —back e.m.f. of motor. l —thermal conductivity of the wires; c —electrical conductivity of wires; f —thermoelectric power of the couple multiplied by T .

THERMAL DIFFUSION ENGINE (FIG. 7)

A hypothetical engine in which pressure is developed between two reservoirs held at different temperatures and connected by capillaries; an ideal gas is assumed to be the working fluid. See E. H. Kennard, 1932. J_1 —heat flux; $X_1 = \Delta T/T$ where T is the absolute temperature.

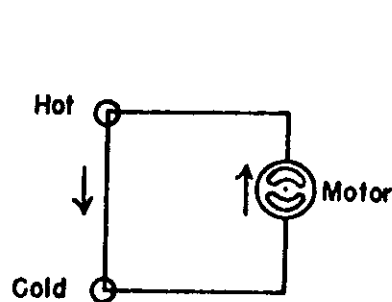


FIG. 6. Thermocouple running an electric motor.

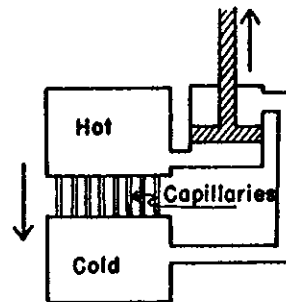


FIG. 7. Thermal diffusion engine; heat source driving a piston.

J_2 —volume rate of flow of gas; X_2 —pressure difference between reservoirs. l and c —both related to cross-sectional area available for diffusion through capillaries; f —calculated from kinetic theory and known as the Soret effect.

METABOLISM OF A PSEUDO-ORGANISM (WITH NO SELF-REPAIR; SEE FIG. 8)

J_1 —rate of glucose utilization; X_1 —free energy drop of catabolism; J_2 —rate of glucose synthesis; X_2 —free energy increase of anabolism. l —taken as zero since no self-repair was postulated; c —related to enzyme rates of reaction; f —unity.

FOOD CAPTURE BY AN ORGANISM FOR ITS MAINTENANCE (FIG. 9)

J_1 —rate of food utilization; X_1 —energy drop in metabolism of captured food units; J_2 —rate of food capture; X_2 —energy drop inherent in the capture of a unit of food; l —basal metabolism spent in self-repair; c —related to the effectiveness of food concentrating method; f —metabolic equivalent of the food capture process.

MODEL OF PHOTOSYNTHESIS (FIG. 10)

J_1 —light energy usefully absorbed per unit time; X_1 —related to concentration of photosynthetic pigment; J_2 —rate of reduction of co-enzymes; X_2 —free energy increase in reduced coenzymes due to an increase in their concentration; l —radiant energy lost as heat if photosynthesis reactions were blocked; c —rates of diffusion and reaction of enzymes; f —related to glucose chlorophyll ratio.

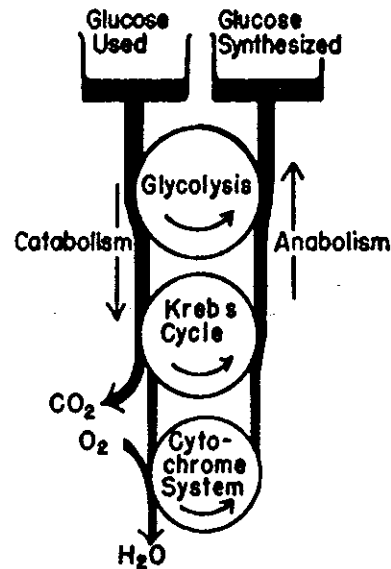


FIG. 8. Pseudo-organism; glucose catabolic enzyme system driving a glucose anabolic enzyme system.

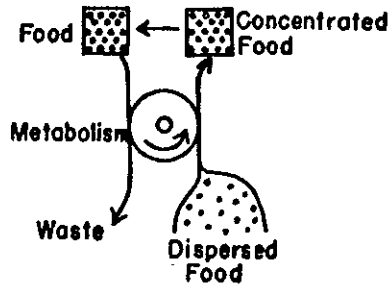


FIG. 9. Food concentration by an organism for its maintenance. Metabolism of concentrated units of captured food drives the process of capturing food.

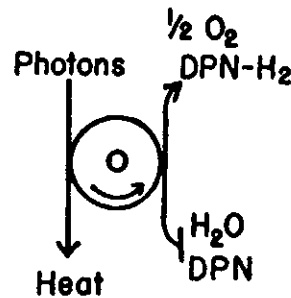


FIG. 10. Model of Photo-synthesis; Absorption of photons drives the reduction of coenzymes.

PRIMARY PRODUCTION IN A SELF-SUSTAINING CLIMAX COMMUNITY (FIG. 11)

J_1 —see above; X_1 —see above; J_2 —rate of plant production; X_2 —increase in available energy per unit community synthesized. l , c , and f as above.

GROWTH AND MAINTENANCE OF A CIVILIZATION (FIG. 12)

J_1 —rate of use of power resources; X_1 —drop in available energy per unit power resource; J_2 —rate of production of value; X_2 —energy per unit value. l —power wastage (water over dams, feeding people, oxida-

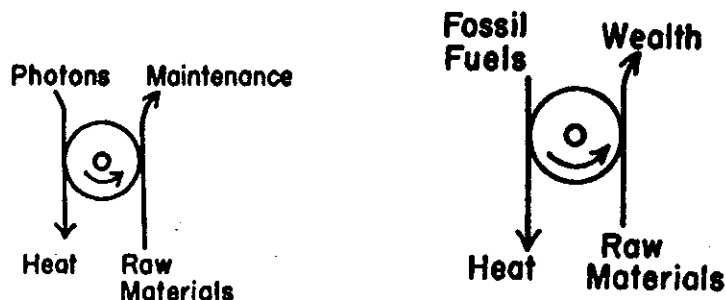


FIG. 11. Climax community. The absorption of photons drives the processes of growth necessary to maintain and repair the community.

FIG. 12. Growth and maintenance of a civilization. The use of fossil fuels in power plants, etc., drives the production of wealth both for maintenance and growth.

tion of coal, etc.) as if maintenance and growth activity were to stop, a state of affairs approached in a depression; c —a function of the productive capacity; f —energy equivalent of value produced.

Coupled Catabolism and Anabolism

The essence of the biochemical workings of an organism is the coupling of an exergonic catabolism to an endergonic anabolism that results in growth, reproduction, and maintenance. Although no organism is as simple as a model, we can construct a model which would be similar from an energy point of view to that pictured in Figure 8. Here the known patterns of glycolysis, tricarboxylic acid cycle, and cytochrome system are paired so that the catabolic flow of glucose into carbon dioxide, water, ATP, and reduced coenzymes on one side is coupled to the resynthesis of glucose. Such systems do occur in organisms although no organism has only these systems. The enzymes which control rates can be readily visualized as controlling the coupling of the two processes so that the maximum power with its accompanying optimum efficiency should result. It is likely that many real organisms have a set coupling arrangement genetically determined, although some enzyme adaptation may involve a quantitative coupling readjustment.

Photosynthesis

In photosynthesis energy of light quanta are absorbed in pigment centers to drive organic synthesis (Fig. 10). If that part of the light actually

absorbed by a functional unit of the organism is considered the input flux J_1 , then some function of the photosynthetic pigment concentration in receptive condition is the thermodynamic force X_1 . When the concentration gradient in the output enzyme system is adjusted to prevent the operation of photosynthesis, then the utilization of absorbed light is stopped. However light may continue to be absorbed, and in this case absorbed light is wasted as leakage as far as organic synthesis is concerned. Leakage may vary with the adjustment of force ratio and, in this instance behaves differently from other cases considered above. As long as the actual workings of photosynthesis are partly obscure, any such hypothesis as is presented here must necessarily be tentative. It seems definite, though, that however formulated, photosynthesis should function like the other processes with respect to having an optimum efficiency and an adjustment of thermodynamic force for maximum power.

The recent collection of reports on algal growth (Burlew, 1953) have fully supported earlier demonstrations that observed efficiencies of photosynthesis are low especially under natural conditions, under large scale conditions, and under moderate or high light intensities. The very high efficiencies reportedly from 50 per cent to 90 per cent observed by Burk (1953) were under very low light intensities and flashing light. The optimum efficiency, maximum power hypothesis seems applicable. From the point of view of maximum plant growth a high efficiency with a very low flux is less important than a flux associated with high power output and a lower efficiency. If this principle is in operation, then the efforts to achieve practical high efficiencies in photosynthesis are doomed, since they can occur only at impractical rates of power output. Man, like the plant, is ordinarily interested in power output, not efficiency.

Under certain conditions in nature where raw materials are supplied at constant and minimal rates, there may be times where a slower but more efficient organism might have an advantage. In fact this efficiency-power relationship may be the basis for understanding some types of successive generations of algae that occur in bodies of water as an initially rich medium becomes depleted. "Poor water" organisms such as some diatoms may be organized for high efficiency and low power output, whereas such organisms as *Chlorella* may be organized for high power output with lower optimum efficiency.

Food Concentration Necessary for Maintenance.

At the organism level, a considerable dissipation of power occurs in the action of the animal in securing and concentrating food which is dispersed in its environment. This is a maintenance requirement of large concentrated systems of living forms with which tiny microorganisms suspended in food may not have to contend with. Sketched in Figure 9,

is an organism which is not growing but is only living in a steady state, balancing food capture against catabolism and other internal maintenance requirements. Here there may again be an optimum efficiency which gives the maximum power output in the form of the food concentrated. In fact the rate of food concentration can be described as a rate of entropy decrease. Possibly this can be made the basis of a rational energetic classification of the process of food capturing. As in the algae, different species may be adjusted for either maximum efficiency or maximum power depending upon the rate of supply of limiting raw materials. There may be different species for each range of the flux of limiting constituent.

Climax Community

In an ecological community that is growing or in one that is being harvested as in agriculture, there is a net increase that can be considered as output power. This output power is much less than the primary productivity which is defined as the rate of organic production by the plants in the community, corrected for daytime respiration. Most of the primary production goes into maintenance of other organisms as well as into maintenance of the plants themselves rather than into community increase or harvests. In agriculture man is continually weeding and spraying to keep the community down to its primary producers only so that he can harvest what would otherwise be leakage and community maintenance.

When the community has passed through its ecological stages of succession and has reached that steady state described by ecologists as the climax, there is no net output and all the energy goes into maintenance, at least theoretically. In this climax example the system is in equilibrium with the output flux J_2 at zero because X_2 balances fX_1 . Thus all the energy coming into the community is completely used by leakage and maintenance.

Under these competing conditions the primary producers, the plants, which are best adapted may be the types that can as a group give the greatest power output in the form of growth. According to the argument given above this should occur when the adjustment of thermodynamic force-ratio of the plants, not of the whole community, R , is 50 per cent. The community of maximum possible size is thus supported. For two climax communities which have similar rates of respiration per unit mass of biological material, the ratios of community standing crops to primary plant productivity should be similar. Thus there is a reason to expect productivity and standing crop mass of biological material (biomass) to have a definite relationship under climax conditions. Communities which do not have the maximum biomass would pass through successive generations until they achieved this condition. One

might expect harvestable crops on a sustained basis only from communities of a successional type rather than from associations of a climax type. This conclusion as a generalization has been noted in many observations by various workers.

Civilizations

The rate of entropy increase in maintaining our American civilization with fuels (Fig. 10) is very great and its efficiency in terms of growth and maintenance may not be large. If the optimum efficiency-maximum power principle applies, then competing civilizations must necessarily have a maximum power output and necessarily a low but optimum efficiency. However, under conditions of limited raw materials as found in many areas of the world, a higher efficiency is the best arrangement although the maximum power output in this example cannot equal the optimum adjustment in which raw materials are not a limiting condition. In a surprising sort of way this seems to be a statement favoring the survival of the spendthrift. The word efficiency is used in this paragraph in the same specific energetic sense as in the rest of the paper, and its meaning should not necessarily be construed in any sense of its desirability.

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