EFFICIENCIES, SIZE OF ORGANISMS, AND COMMUNITY STRUCTURE

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In the following paragraphs are presented some unproven ideas and concepts about communities and their adjustment in natural circumstances. Although it is presumed that there will be many exceptions, these concepts are proposed tentatively as generalizations. It should be emphasized that where the types of behavior discussed here are meant to apply to whole communities, they do not necessarily refer to the functions of single organisms.

HUMP-SHAPED RELATIONSHIP OF PRODUCTION AND EFFICIENCY WITH VARYING LIGHT INTENSITY

In Figure 1, the production rates of natural plankton communities in a lake obtained by Manning, Juday, and Wolf (1938) at several levels are plotted as a function of efficiency of photosynthesis. Also indicated are the properties of production and efficiency obtained in much of the work that was done on the quantum requirements of algal cultures where low light intensities were used. The curve is hump-shaped. As discussed below, it may be suggested that a hump-shaped relationship of production and efficiency is general when only the light intensity is varied. At low light intensities, in spite of high efficiencies the energy flow is so small that the production is small. At high light intensities the production is greater in spite of lowered efficiency.

That no natural community, agricultural plot, or experimental situation resembling nature has apparently achieved high efficiences above 10% under full daylight intensities may be interpreted as an evidence for the inverse relationship of efficiency and production that occurs on the right-hand portion of the hump-shaped curve. (See data in Rabinowitch 1951). Another example was the effort made to achieve high efficiencies under natural light conditions in culture efforts (Burlew, *et al.* 1953) which was not successful.

OPTIMAL EFFICIENCY-MAXIMUM POWER HYPOTHESIS APPLIED TO PRIMARY PRODUCTION

If curves like that in Figure 1 are typical, there is a maximum production associated with the peak of the curve and an associated relatively low efficiency that is optimum. If the primary production of communities is important for their competitive survival (Lotka's principle), there will be a tendency for communities to

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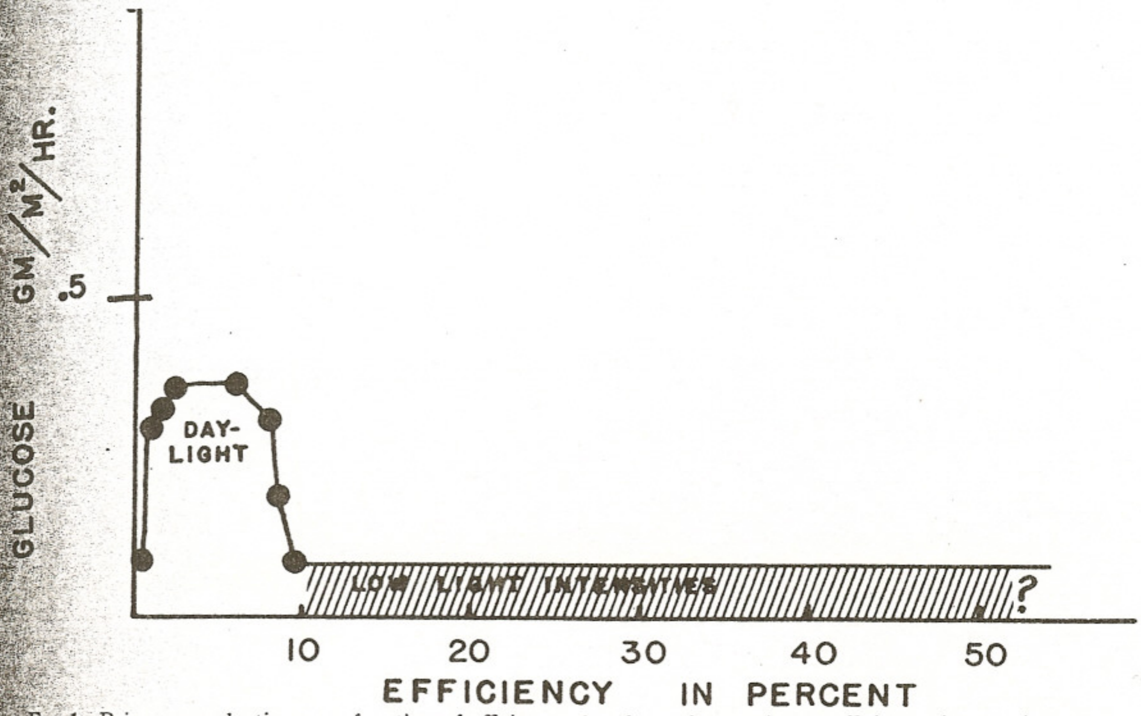

FIG. 1. Primary production as a function of efficiency showing a low optimum efficiency for maximum power output and a low power output with maximum efficiency. The plotted points are from bottle experiments in lake water by Manning, Juday, and Wolf (1938). Values for high efficiencies but low production are summarized in Rabinowitch (1951).

be adjusted to that production and efficiency corresponding to the peak of the hump-shaped curve. There is thus a reason to expect somewhat similar low efficiencies among many successful naturally-adapted communities, although the exact position of the peak may be a function of nutrient and carbon dioxide levels.

In accounting for the hump-shaped curve of production and efficiency, we turn to the basic nature of energy transfer as expressed in the second law of the thermodynamics. In a theoretical derivation given elsewhere (Odum and Pinkerton 1955), it was demonstrated that for simple physical systems under certain proscribed conditions, the second law of thermodynamics required a hump-shaped curve of power and efficiency. Although there is apparently no question of the validity of the principle for simple physical systems, the application to more complex biological systems like community photosynthesis is hypothetical. However, it is proposed that the hump-shaped type curve of Figure 1 is typical, and rooted in the second law of thermodynamics. If the principle is general, attempts to calculate increased world food potentials on the basis of efficiencies obtained in low light experiments should cease.

THE APPLICATION OF THE SIZE-METABOLISM GENERALIZATION TO PHOTOSYNTHESIS

That the metabolism per gram of heterotrophic organisms is inversely related to body size in a somewhat varying ⅔ power function is a rough generality possibly based on the surface-volume limits to various diffusion processes (Zeuthen 1953, Bertalanffy and Pirozynski 1953). The importance of size effects in determining rates of turnover in zooplankton populations has been discussed by Harvey (1955). Let us now consider size effects in the phytosynthesis of the plants.

In the previous section, a reason was given for expecting naturally adapted, competitive communities to develop similar, moderately low efficiencies when adjusted to similar light regimes. Here efficincy is defined as the per cent of absorbed light of usable wave length that is converted into organic matter. If communities (not individual plants) tend to develop similar photosynthetic efficiencies, there will tend to be similar total photosynthetic power outputs of glucose on an *area of community* basis. This reasoning is based on the tendency for adapted communities to develop sufficient depth of chlorophyll-bearing tisses to absorb most of the available light. The similar efficiency of about 2.5% found for both *Chlorella* cultures and adjacent grass plots (Wassink, *et al.* 1953) is a good illustration of the tendency for similar productive rates to develop in adapted communities.

Suppose the producers do tend to metabolize at the same rate of output per area of community, and suppose size effects hold for photosynthesis as well as for respiration. Then, communities made up of small plants like *Chlorella* growing in steady state should sustain only a small standing crop biomass at any one time in order to achieve the same output per area exposed to the sun as communities with larger plants. Conversely, the big plants in climax rain-forest communities should require a much larger standing crop of photosynthetic biomass to achieve the same production because of the slower metabolism per gram of tissue. Next, we ask if there is any factual basis for the proposed inverse relationship of photosynthesis per gram and individual size in naturally adapted communities.

In Figure 2, aquatic photosynthetic rates on a gram basis under natural light or maximum photosynthetic adjustments are plotted from Verduin (1952) as a function of size. Some aquatic leafy plants are also included

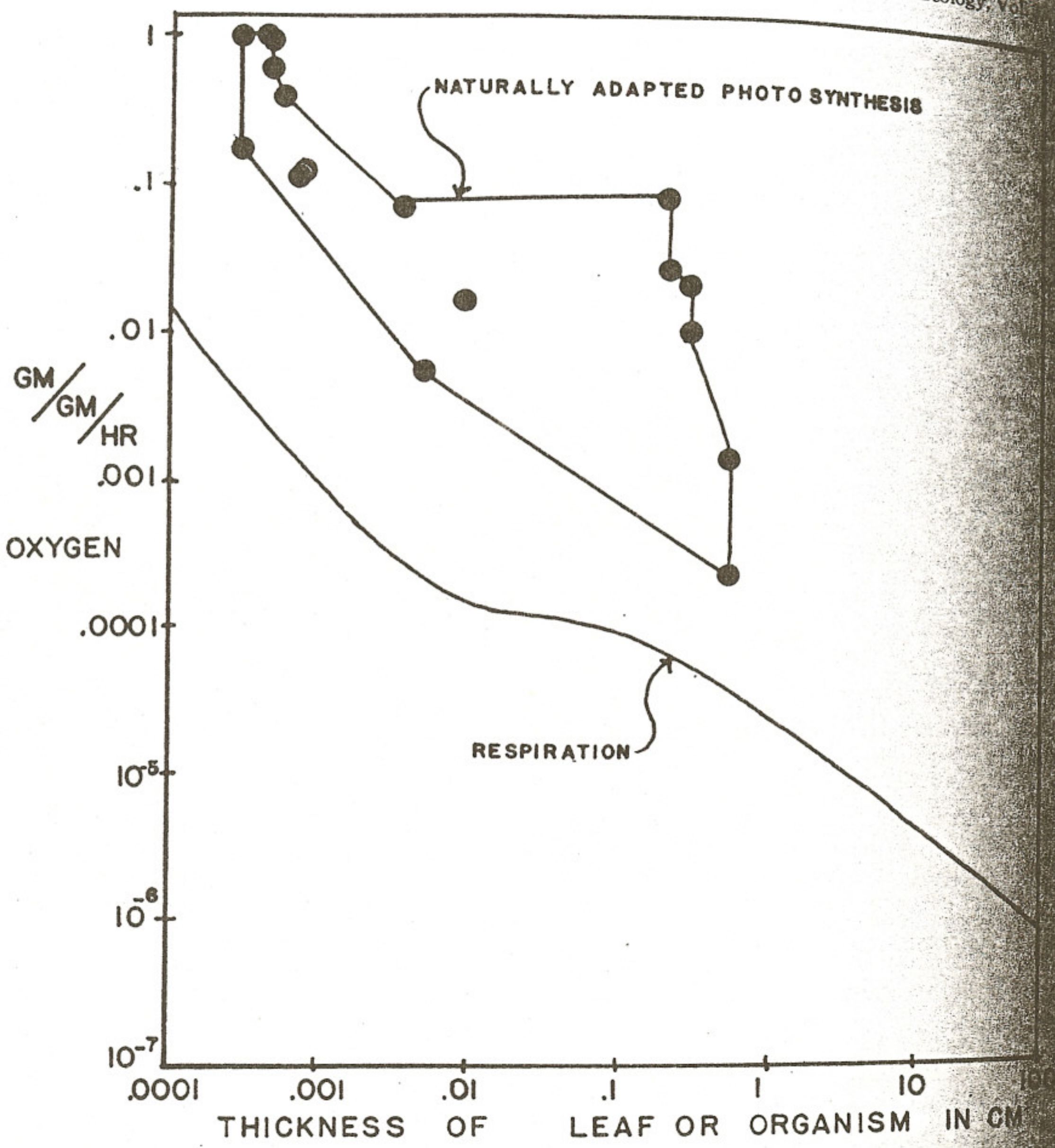

FIG. 2. Metabolism per gram of biomass as a function of organismal size. A line summarizing respi
of heterotrophic organisms was obtained from data in Figure 1 of Zeuthen (1953). The points repres
naturally adapted photosynthesis were taken from data collected by Verduin (1952).

with the appropriate leaf thickness being used as size. It is quite apparent from the graph that there is a size effect over a wide range of size just as in respiration processes. The slope is not inconsistent with the slope for animal and bacterial respiration as obtained from Zeuthen (1953). Thus, if one knows the light intensity, the size of the producer, and the rough efficiencies usually found in natural communities, one can compute the potential steady-state biomass (carrying capacity) without direct empirical measurements. At least, one has a basis for obtaining orders of magnitude theoretically without even knowing the species involved. If valid, this could be a useful process of general geography and practical conservation where estimates must be made for large areas where empirical measurements have not been made.

Biomass Pyramid Shapes and Productio

Pyramids of biomass are convenient graphic
representing the standing crop (stock) of comm
according to their trophic levels, but a general s
has not been made to indicate the kinds of pyram
are possible in different situations. Whereas
vironments have more producer biomass than
biomass (Odum 1953, Odum and Odum 1953
in other communities, such as in planktonic
ties, the pattern may be reversed. Some of
cepts given in the preceding paragraphs are in
low in an attempt to summarize the relatio
pyramid structure and production rates under
conditions.

Three principal mechanisms are important in regulating the expression of production in the standing crop. One is the ratio of the animal consumers to the bacterial consumers. The second is the distribution of organismal size relative to the trophic levels. The third is the relative quantitative dominance of gross primary production (P) and community respiration (R) as represented by the P/R ratio.

To illustrate the working of each effect separately from the others, some pyramids of biomass have been calculated in Figure 3. In Figure 3c, the effect of increasing organismal size up the food chain is compared with decreasing organismal size up the food chain. In this example, half of the primary production has been assigned to bacteria, which due to their small size and hypothetically large metabolism are for practical purposes invisible components. Metabolic values for the bacteria were taken from the respiration line in Figure 2. In these two pyramids, a P/R of 1 implying no net imports or exports was assumed.

In Figure 3b is shown the effect of different ratios of decomposers (bacteria) to other consumers. A constant organismal size for all non-decomposer trophic levels and a P/R of 1 are assumed for this example. It is clear that the larger the bacterial component, the smaller is the mass of consumers supported since the bacteria tend to be negligible as standing crop biomass.

In Figure 3a are shown pyramids illustrating the effect of different quantities of imports and exports. A case is shown with large imports ($P/R < 1$), one with self-sufficiency ($P/R = 1$) as in two previously discussed groups of pyramids, and one with a net export ($P/R > 1$). Here, bacteria have been assumed to get half of the primary production, and size has been assumed to be the same for all trophic levels. Here the higher P/R ratios give the lower biomass in the consumer trophic levels. A community which is either exporting or storing organic matter (in excess of its imports) tends to have a small top. Harvestable agriculture, successional communities, and communities building up organic sediments are of such type. Silver Springs is an example of a case where the organic matter is exported downstream. The other extreme is represented by a sewage polluted stream, where the large imports relative to exports can support a considerable biomass that is not based on a photosynthetic energy supply. P/R measurements of stream communities are given elsewhere (Odum 1956).

In most communities, the three effects described above are all in operation. The types of pyramids that result under these interacting circumstances areas are as yet little known. As data become available, calculations like those in Figure 3 will permit one to estimate unknown phases of community metabolism from the standing crop. For example, from production measurements, from the organismal sizes, some idea of the invisible parts of the community, the bacteria, may be computed.

Criticism of Some Definitions of Consumer Productivity

In an imaginative paper, Lindeman (1941) quoted Hutchinson's formulation of the relationship of standing crop (Λn) to energy intake (λn) and energy loss ($\lambda \acute{n}$) for trophic level n as follows:

$$\frac{d\Lambda n}{dt} = \lambda n + \lambda \acute{n} \qquad (1)$$

As seen in the energy flow diagram in Figure 4, there are too many major routes of energy flow through each trophic level for the above scheme to be applied. However, Lindeman applied these concepts to several communities by making the quantity (λn) in the above expression serve as a definition of production. In this procedure, a very misleading and inconsistent usage was begun which if not actually incorrect has created an apparently unrecognized confusion in the definition of production. In the top diagram in Figure 4 Lindeman's usages of symbols of equation (1) above have been added to an energy flow diagram previously used by the present author as a convenient method of clarifying concepts of community energetics (Odum 1956).

The inconsistency in Figure 4a is in the use of the symbol for production in the sense of rate of synthesis of organic matter in the first trophic level while using this symbol in the consumer trophic levels to mean production in the sense of energy intake (consumption, assimilation).

In a series of otherwise clear formulations of production concepts, Clarke (1946, 1954) has used a set of bar diagrams to show the fate of the energy which enters a community as sunlight. Just as was done by Lindeman, Clarke has defined production for the herbivore and carnivore trophic levels as the rate of energy uptake. These usages by Clarke and Lindeman have been widely quoted and included in reference sources such as Allee, *et al.* (1949).

In contrast, the principal idea of production is widely accepted as the rate of synthesis of organic matter whether by plants or animals. To use the term production to mean rate of energy intake is quite contrary to the ordinary English usage as well as its ecological usage by many.

The difficulty in part comes from attempts to divide production processes at a consumer trophic level into gross production and net production just as is done for the primary producer trophic level. In the primary producer trophic level, the gross production is the total result of autotrophic photosynthesis and can be measured by oxygen release. The net production is the organic synthesis remaining after plant respiration has dispersed some of the gross production as heat. In the higher trophic levels however, there is no process comparable to gross production of the primary producers. There is only one measurable production, the net growth and organic synthesis that results from heterotrophic metabolism based on ingested food materials. To assign the term gross production to consumer assimilation (energy intake) is to make production synonymous with total metabolism (respiration plus synthesis). This is no more pertinent than considering the rate of fuel consumption of a bonfire as the production of the bonfire. One possible source for this objectionable viewpoint is the mistaken notion that all of the energy that enters an animal is transformed into new organic matter or equivalent useful work before being expended as heat. Such an assumption is contrary to the second law of thermodynamics.

It is thus suggested that consumer production be defined as rate of new organic synthesis rather than as rate of consumption. In Figure 4b are given a set of symbols in a more consistent usage with I_n for the energy intake, R_n for respiration and P_n for the new organic synthesis (net production) for trophic level n. P is the gross primary production. In this usage, there is no gross production beyond the producer trophic level. Since the primary production trophic level differs from the consumer trophic levels by having a double energy transfer, concepts and symbols must indicate this difference.

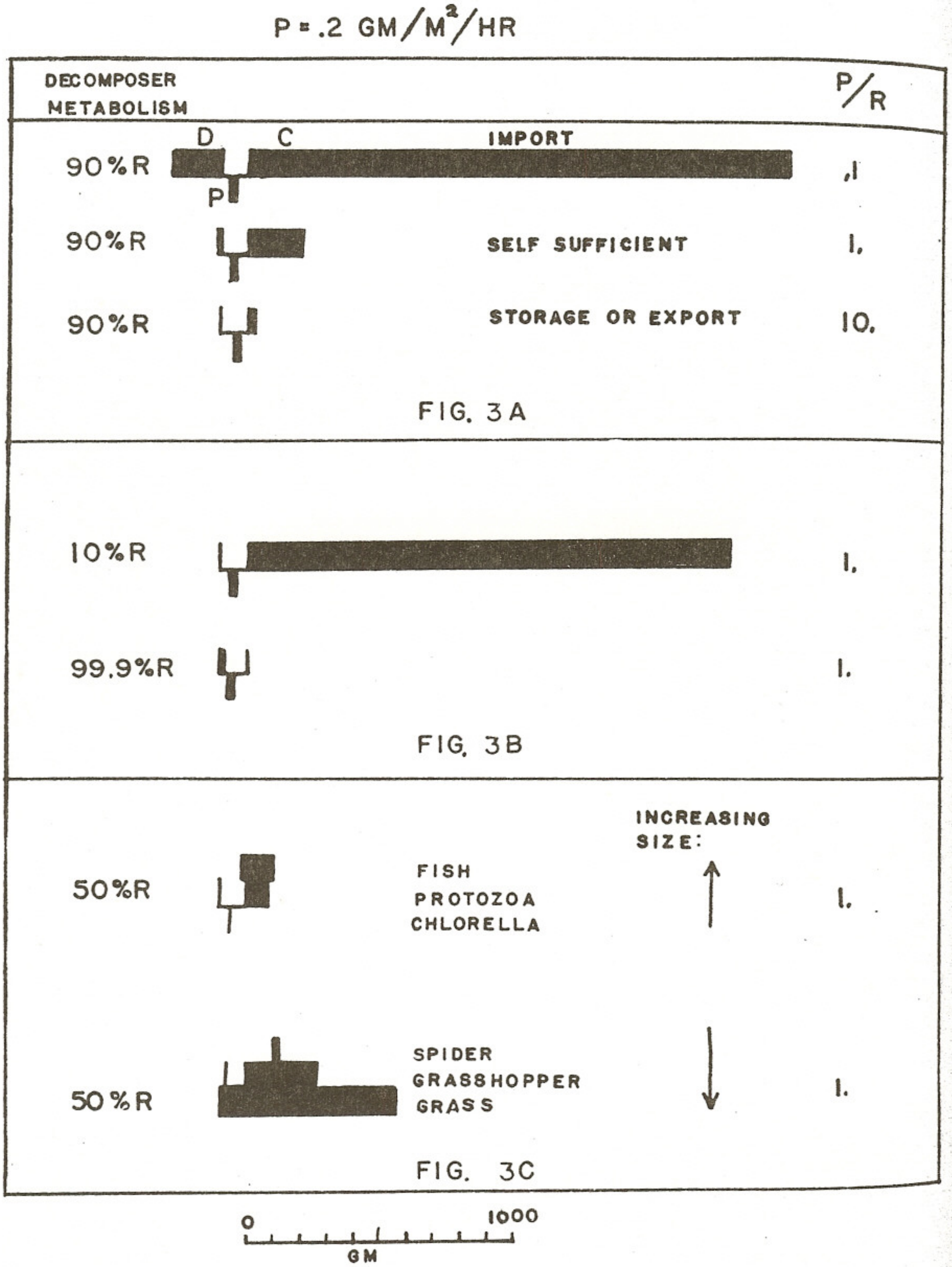

Fig. 3. Biomass pyramids (grams dry weight/m²) under steady state conditions as a function of export-import balance, per cent decomposers consumption, and organismal size. Each pyramid is based on the same primary production (0.2 gm/m²/hr) on an area basis. The standing crop biomass of producers (p) is indicated to scale as the lower bar of each graph. The decomposers (d) and other consumers (c) are indicated by the two bars at the level above the producers. The third level in Figure 3c refers to the carnivores. The ratio P/R indicates the ratio of gross primary production to the total community respiration. The fraction

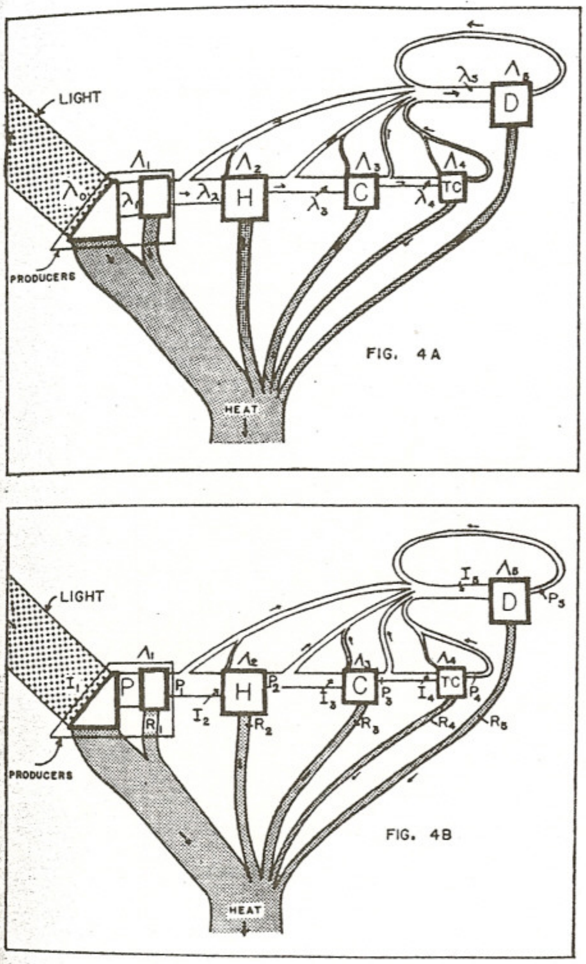

FIG. 4A

FIG. 4B

FIG. 4. Energy flow diagrams for a community with 5 trophic levels without export or import. The flow of energy into the plants as light eventually passes via shaded routes out from the community as dispersed heat. Trophic levels are represented by the heavy squares. The primary producer trophic level contains photosynthetic and respiratory divisions. The trophic levels are indicated by H, herbivores; C, carnivores; TC, top carnivores; and D, decomposers. Unshaded routes indicate the passage of energy as transferred organic matter. Production is indicated in the horizontal pathways; unassimilated consumption and decomposition routes lead upwards to the decomposers.

In Figure 4A, Lindeman's use of Hutchinson's symbols are given (see text). In Figure 4B, I_n represents energy intake; P gross primary production; P_n net production; R_n respiration; and Λ_n the standing crop of trophic level n.

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of the total respiration due to decomposers (bacteria) is indicated on the left column. Estimates of bacterial metabolism rates were taken from Figure 2.

3a. The relative dominance of consumers in the standing crop is quantitatively related to the P/R ratio. Nonbacterial consumers of the same organismal size as the producers were assumed.

3b. The relative dominance of conspicuous consumers is quantitatively related to the percent of the respiration due to bacteria. Nonbacterial consumers of the same organismal size as the producers were assumed.

3c. The shape of biomass pyramids is controlled by the distribution of organismal size in the food chain because of the increasing metabolism per gram with decreasing size shown in Figure 2.