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Workshop agroecology

Paris : CIHEAM
Options Méditerranéennes : Série Etudes; n. 1984-I

1984
pages 161-166

Margalef R. **Summary of the main arguments from a theoretical perspective.** *Workshop agroecology*. Paris : CIHEAM, 1984. p. 161-166 (Options Méditerranéennes : Série Etudes; n. 1984-I)

SUMMARY OF THE MAIN ARGUMENTS FROM A THEORETICAL PERSPECTIVE

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Key Words: Theory, Ecosystems, Primary Production, Physiology, Global, Energy.

ABSTRACT

In summarizing the papers and ideas presented in the workshop from a theoretical perspective several general observations can be made. First, evolution has led to parsimonious use of energy and, therefore, to assume a trend to maximize energy is more a reflection of human culture than a natural strategy. Second, the low level of the upper limit to primary production is a response to the physiological basis of photosynthesis and the factors limiting production. External energy forces and controls the flow of internal energy through evapotranspiration on land and through bringing materials up to the photic zone in water. Third, availability of external energy is related to scales of time and space. Fourth, management opens these ecosystems, accelerating turnover, and segregating or separating essential resources from use.

RESUMEN

Al resumir los informes e ideas presentados en el simposium desde una perspectiva teórica, se pueden formular varias observaciones generales. Primero, la evolución ha llevado a un uso parsimonioso de la energía y, por tanto, asumir una tendencia a maximizar la energía es más un reflejo de la cultura humana que una estrategia natural. Segundo, el bajo nivel del límite superior de la producción primaria es una respuesta a las bases fisiológicas de la fotosíntesis y a los factores limitantes de la producción. La energía externa fuerza y controla el flujo de la energía interna por medio de la evapotranspiración en la tierra y de la extracción de materiales hacia la zona fótica en el agua. Tercero, la disponibilidad de la energía externa está relacionada a las escalas de tiempo y espacio. Cuarto, el manejo abre estos ecosistemas, acelerando el turnover, y segregando o separando los recursos esenciales de su utilización.

In a *post factum* reflection, the purpose of this workshop seems to have been to use the knowledge gained through the study of natural ecosystems to interpret the workings of the agroecosystems and to improve their exploitability. On the converse, study of agroecosystems is often helpful to understand natural ecosystems. Bridging between both areas of study, concerning natural and humanized ecosystems, proved a fruitful exercise in global ecology, and it is my assigned duty to pinpoint and comment on some theoretical questions arising.

My treatment, and even the whole workshop, may offend practical people, including many agronomists and foresters, who tend to see man and nature as dialectical opposites, and also ecological activists, who dream of token parts of the biosphere, uncontaminated by civilization, at least as tranquilizers of conscience. We have to accept man as a substantial part of the biosphere of today, and in the workshop it has been pointed out frequently how economic, social and political facts are essential to understand and follow problems up to the level of a global ecology.

A number of mostly unresolved questions that have appeared along the discussions, have been combined and organized in a few headings of this summary. This procustrean procedure has the aim of proposing objectives for future research, and the less practical purpose of showing how problems born in separate contexts can be related, to help new developments in ecology. My personal work explains the frequent reference to aquatic ecosystems for the purpose of comparison.

PRIMARY PRODUCTION. THE NATURE AND ORGANIZATION OF THE PRIMARY PRODUCERS

Living beings are miniaturized and by reasons of scale require energy of high quality, as light or in the chemical bond. Only a small fraction of the available solar energy, less than one per thousand, is involved as endosomatic energy in biological production. Evolution has led to a rather more parsimonious than frantic use of energy. To assume a trend to maximize flow of energy is, in my opinion, a natural reflection of the puritan ethics of work. The organization of primary producers sets at an amazingly low level the upper limit to primary production.

Empirical data

A review of the data on primary production shows that the value of 1.5 g C m^{-2} h^{-1} is rarely, if ever, surpassed. Maximum primary production may be 5000 g C m^{-2} $year^{-1}$, but the average on land is probably close to 300 g C m^{-2} $year^{-1}$ net production, and the average for the oceans 100 g C m^{-2} $year^{-1}$. The main reason for the difference is the longer path to recycling imposed by the average depth of the marine environment, and also the different organization of the transport system: turbulence and animals at sea, trunks, roots and fungi on land.

Physiological basis

The number of molecules of chlorophyll in the antennae, for each reaction center (200 to 600) is an extremely conservative feature in plants. As a consequence of the packing of chlorophyll, under usual illumination a large proportion of the photons are unused. Only in some mutants of *Chlorella* and in the heterocysts of cyanobacteria, the number of molecules of chlorophyll per antenna may be unusually lower, promising, incidentally, the possibility of some genetical engineering approach to "improve" efficiency in primary producers, although this would imply a total reconstruction in the organization and function of plants. But this would be of more consequence than the introduction of the possibility for N_2 assimilation.

In appropriate conditions of light and nutrients, 1 g of chlorophyll could yield per hour a number of g of organic carbon that has a theoretical maximum of 25, an empirical maximum of 11, and an effective maximum value between 3 and 4, if the limitations of the real distribution of light through the thickness of the assimilating volume are taken into account. In aquatic cultures and natural ecosystems, about 400 mg of chlorophyll is the maximum that can be effective over 1 m^2, as this amount absorbs practically all the light. In consequence the highest primary production per square meter should be $400 \times 3.5 = 1.4$ g C $hour^{-1}$, in good agreement with observation. This concept of a maximum of functional chlorophyll in relation with the absorption of the pigment is obvious in aquatic ecosystems. Perhaps not as much in terrestrial systems, including agroecosystems, where the concentration of chlorophyll is about the same (400 mg m^{-2}) in relation to the extension of the leaves but the leaf index is above one, frequently around 4, and often much higher in natural vegetation. This excess of pigment suggests a different, and perhaps more effective, utilization of light, involving multiple reflections of the major part of it on the moving leaves.

Factors of production

Synthesis of organic matter requires a number of elements. Appropriate concentrations and a high covariance among the concentrations of the different nutrients (including water) makes production high and uniform; low covariance or segregation of the residuals shows that utilization is going to the limits. In terrestrial plants, water is the carrier of nutrients other than CO_2 and the ratio between water transpired and dry matter assimilated is dependent of the concentration of nutrients in soil water, and usually is in the order of 500. The organization of plants is often presented as centered on the need to reduce loss of water, but in fact the more water one plant passes, the better. Evapotranspiration is closely related to exosomatic energy. The plants with non standard forms of metabolism concerning CO_2 (C_4, CAM) may represent converging adaptations to decreasing CO_2 contents in the atmosphere; the new properties are specially advantageous in the secondary growth of tropical moist countries, and are much appreciated in cultivated plants. The natural analogy of this situation in aquatic plants is the adaptation to use bicarbonate; plants able to do so, in alkaline water outcompete primary producers that require CO_2. *Chlorella* is a frequenty cultivated green alga; in water of medium and high alkalinity it is outcompeted by *Scenedesmus*, and it pays to prepare a culture medium with the capacity of retaining an important amount of inorganic carbon, that is made available to the algal cells.

Different availability of nutrients lead to particular situations in natural ecosystems, as well as in agroecosystems. In lakes and reservoirs with a rather high calcium content, phosphorus may become particularly scarce in summer, and the ratio N:P is relatively high. Chlorophyceae are common in such situations, nitrogen stimulates the normal synthesis and function of chlorophyll, but lack of phosphorus limits multiplication of the cells. As a consequence, cells synthetize and excrete large amounts of carbohydrates, either in form of soluble small molecules, or as longer molecules and in the form of mucilagineus envelopes. The mucilage covers may limit diffusion and operate, in consequence, as controls of population growth. The example has a counterpart in the extensive cultures on poor Mediterranean soils, also with low availability of phosphorus, with vineyards and olive trees (with more water also sugarbeets), where the yield consists in a great part of compounds of carbon with no more substance.

Global cycles

The activities of the ecosystems are reflected in the balance of CO_2 and O_2, also in the atmosphere. Most systems are balanced over themselves, and the role of the ocean and the forests has often been misconstrued. The producers of oxygen are the crop fields, the eutrophic lakes, the upwelling areas, contrary to the popular belief. One per cent of the organic production of the continents goes to the oceans, which may be slightly stressed or heterotrophic.

The normal working rate of the ecosystems and the durability of organic matter lead to a ratio between dead organic carbon and living organic carbon that may be of the order of 10. The appropriate symbol of the biosphere is a large dung beetle that turns a pill several times its own weight. The dead organic matter is a store of energy, as is obvious in fossil fuels, and still more expressive in the sediment of lakes, which acts as a storage battery in the circulation of energy associated with redox gradients. Man, through erosion and exposure of dead organic matter, use of fossil fuels, and destruction of supporting structures of plants, is changing in a noticeable way the existing ratios. These changes, together with the capacity of the sea to absorb CO_2 are the big unknowns in the task of trying to foresee changes in the CO_2 content in the atmosphere.

THE ENVIRONMENT: EXOSOMATIC ENERGY AND ITS DISTRIBUTION IN SPACE AND TIME.

External energy

Energy provides a common and convenient measure for most of the environmental factors. External or exosomatic energy forces and controls the flow of internal or endosomatic energy, or primary production. This is clear in what concerns terrestrial environments. The evaporation of 200 - 1000 kg of water for each kg of assimilated organic matter sets the ratio between external and internal energy between 25 and 150. In aquatic environments, the energy involved in bringing nutrients back to the photic zone stands in a similar relation to primary production. The world distribution of upwelling areas and of marine productivity generally, as well as the strong dependence of terrestrial production on rainfall, testifies to the dependence of productivity on locally available exosomatic energy. The same is true in the dependence of yield on the energy subsidy (work, watering, fertilizers) in agriculture. The energy is important in the horizontal transport, erosion and availability of nutrients; just compare productivity of tropical forests in slopes and on the plain. Response to external energy follows the law of diminishing returns, and too high inputs may have a disorganizing effect, unless the internal organization of the system can cope with them.

Internal energy, stored in organic matter, can work later as external energy, as in forest fires or in the use of fossil fuels by man. Man is increasingly developing a system of switches and multipliers in the manipulation of the natural sources of energy that work as exosomatic energy on the biosphere, and these effects, nowadays, may be of more consequence on the future of biosphere than simple exploitation. Part of this external energy under the control of man helps to enhance primary production in systems controlled by man, but, as David Pimentel has shown us, still more energy is invested in getting rid of wood, consumers and competitors, in other words, in preventing selforganization of ecosystems and in maintaining them exploitable.

Space spectra

Availability of external energy is related to scale. In aquatic ecosystems, wave development requires a fetch, upwelling systems require large gyres and corresponding wide oceans; probably no modern aquaculture systems make sense now if below a minimum size. In terrestrial ecosystems overall transport over entire landscapes is related to orogenesis, topography and, absolutely, to size.

If external energy is at a low level, and uniform, ecosystems can be modelled as a set of narrow prisms or columns, side by side, roughly equivalent, and with no transport, or at least no net transport (symmetrical exchanges across the adopted and ideal boundaries). This is the local form of stability that goes associated with the slogan "small is beautiful". Under stronger external energy and more important horizontal exchanges, it is no more possible to conceive as isolated the local spots, which are strongly linked with the neighboring areas as much as the horizontal transport driven by external energy allows. This is obvious in heterogeneous environments, subjected to high energy inputs, as in mountain landscapes, or in floodplains and in marshes. In human terms this situation is easily identified with the functional differentiation between rural and urban areas, much dependent on external energy for support, but with certain advantages that justify the slogan "big is powerful". One advantage? Is that, over large spaces, it is relatively cheaper to prevent autoorganization and reconstruction of natural ecosystems, and to preserve exploitability; but erosion can become more dangerous.

In general, man gets the source of energy in one place, and uses it to do work in another, usually at a higher latitude. Will this upset the natural balances, or is it easily absorbed and equilibrated in the workings of the global thermic machine?

Time spectra

Much external energy does not flow continuously. We have day and night, summer and winter. Time and space discontinuity is capital to understand the workings of the oceans. Weather fronts are important in temperate agroecosystems. The spectrum of disturbances goes up to glacial periods, plato tectonics and impacts of planetoids. Frequency of inputs is inversely related to the intensity of the disasters, the reason why what is more important is as well the most impredictable.

The essence of the resulting mechanism is provided by the asymmetry of events around the impact time. Any sudden change is followed by a slow recovery that can be identified frequently with ecological succesion. Evolution seems to be directed to overcome impacts more and more important, so far this is worthwhile in relation with their frequency and the life length of the individuals. We care for seasons, start to worry about climate changes, but cross simply the fingers before the menace of meteorite collision —and even of nuclear war—. On a lower level, relation between production and biomass is very much related to the spectrum of disturbance and its manipulation has been a key instrument in the management of agroecosystems.

MANAGEMENT: OPEN THE SYSTEMS, PREVENT THE PROCESS OF ORGANIZATION AND EXPLOIT

Ecological succession consists in the capitalization of the excess production, until total respiration matches production. Later, some rearrangements are possible, probably in the sense of maximizing the biomass that can be supported by a rather surprisingly restricted flow of energy. Exploitation from outside has to preserve primary production at the same level, if not higher, and make away with most of the non assimilating and respiring components of the ecosystem, not only animals, but also most of the supporting tissue of plants, as in the success story of the green revolution. Exploitation counters succession and is incompatible with any extreme conception of conservation. Nature, by itself, tends to become more complex, and, as any bureaucracy *comme il faut*, to use finally all the resources in its own maintenance.

Agriculture and aquaculture keep open the systems, take out materials, and prevent the growth of an organization. In such conditions, biological control, as usually understood may be of doubtful consequence. Management includes the interruption of organized transport inside the system, the vertical transport in the trees, and the horizontal transport in roots and fungi of the soil. Simplification of connections means the replacement of the old hierarchy by a new hierarchy that benefits the exploiter.

Exploitation can be conceived as well as a stress applied to the ecosystem. The two major responses to stress are: (1) acceleration of turnover, which is good to the exploiter, and (2) segregation of one fraction of the cycling materials at or across the boundaries (oxygen and nitrogen to the atmosphere, phosphorus in insoluble state in the soil), and this is not as desirable. Perhaps it is wise to refrain from speaking of equilibrium and of maximum sustainable yield.

A number of natural ecosystems are preadapted to sustain exploitation, since they have developed subjected to natural exploitaton, active or passive, like upwelling areas in the ocean, grasslands, the temperate forest and its clearings, marshlands. Ants, termites and rodents, as well as large herbivores, helped to create simplified vegetations with essential characteristics of agroecosystems. Species exploitable by man have evolved in environments of the same characteristics, sardines and anchovies in upwelling areas, grasses with massive and seasonal production of diaspores. All the biosphere follows the same regularities and the appropriate ways to improve exploitability pass through a better understanding of the functioning of natural ecosystems. Destruction of spontaneous structure and use of information, in picking weeds, use of selected strains and rigorous controls of the times of watering and fertilizing, can be still improved, besides a perhaps more wise recourse to chemical warfare. Tropical ecosystems, except the montane and the marshes, pose, in general more serious problems that are conceivable in the frame of the general theory of the development of ecosystems.

In natural ecosystems, fluctuation is good, if unwelcomed, as such fluctuations have been the cause of selection and of maintenance of positive qualities in exploitable species, as the sardines. In the Mediterranean, fertilizing events fluctuate in a somehow independent way, and the total variance in the effectivity of fertilization is reduced. This, perhaps, makes the system less exploitable. From the point of view of man, the exploiter, reactivity and horizontal exhange are more interesting than rich diversity and vicariance of species in a field of low energy. Thus we are led to monocultures, and cannot tolerate weeds.

Evolution in plants has resulted in organisms able to produce a durable transport system, made of materials of low degradability, as cellulose, hemicellulose and lignin. No two trees are alike, and each tree is comparable rather to a culture than to an individual. A trunk, indeed, may be compared with the system of transport and communications linking the residence places of social animals, like termites and man. Trees control transport and external energy, using rain as well as wind and light. They remain in place, starting the season with impresive local occupation and control, an ecological equivalent of the inmigration of birds in the northern spring. They control the materials being forwarded to other compartments of the ecosystem (litter), can take nutrients away from herbaceous plants, with the same effectivity as a crocodyle stores phosphorus in the varzea. Trees prevented effectively the heterotrophs (including animals) to take over in the way they have done in the aquatic environment, until man came with fire and ax.

But wood is a useful resource, worthy of exploitation. The ideal wood would contain only carbon and water. Exploitation of forest requires fertilization or natural replacement of nutrients through rainfall and runoff. A serious effort has to be done to integrate forestry and ecology.

SUBJECTS OF COMMON INTEREST.

Three subjects of a more general and theoretical nature have to be mentioned and recommended for further consideration.

Models

The usual approach to modelling has to be improved. Simple clock work models, even allowing for stochastic inputs, are not enough. No machine turns twice being exactly the same, much less an ecosystem that continuously converts energy into structure. On the basis of the consideration of plankton systems, I have been led to propose (Margalef, 1978; in press)

$$\underset{\text{production}}{P} = \text{inputs} + \underset{\text{turbulent energy}}{A} \times \underset{\substack{\text{Covariance of the}\\ \text{distribution of the}\\ \text{factors of production}}}{C}$$

an expression that perhaps allows a more general application. It is, of course, a spectral expression, since inputs of non renewable resources can be easily internalized when the spatial frame of reference is enlarged. Turbulences and covariances demand also a spectral expression. With reference to time, succession is well described with negative values of the following tems

$$\underset{\text{deceleration}}{dP/dt} = \underset{\text{decay of energy}}{a\,dA/dt} + \underset{\text{ecological segregation}}{b\,dC/dt}$$

Management of agroecosystems tends to counter deceleration, and this is done introducing resources from outside, controlling energy, and simplifying and uniformizing the distribution of the components of the system.

Information

Information is seen as a limit, but its effectivity and use inside such limits is hard to prove. For man it means organization, capacity to organize, know how, and aptitude to learn. In the workings of the ecosystem the meaning becomes understandable. We have a flow of internal energy, coming into the primary producers, and from them to other trophic levels, with a strong and decreasing loss. Information appears to be more important, or more congenial with our own concept of information, towards the top of the trophic ladder. This is in part by reasons of size (a computer twice as large is more powerful than two computers standard size), and of length of life. The noncoincidence of the energy decay with the places where information is more effectively accreted is perhaps one of the most striking properties of systems and ecosystems. It can be visualized at the level of elementary interactions: an insect is selected for the expression of some defensive property against a bird; a bird is selected in its relation to the insect by its capacity to learn. Probably learning is more effective if the environment is complex and changeable. And man can be aptly characterized as an organism able to learn to learn to learn.

People

Everybody agrees that the main problem is people. People, now, not only as exploiter and consumer of resources, but also as wielding the control of important flows of external energy. If population changes at the rate r, and individual use of enegy at the instantaneous rate f, the total use of energy increases as the exponential of $r \times f$. This sum has to go down to zero, in any reasonable prospective of future, and this relates understandably with the projects of future use of resources and operation of external energy.

At present, in rich countries f is on the average more than two times r; in poor countries the inverse relationship prevails. It would be desirable that present values of r and f converge, through a reasonable path, and as fast as possible, to the line of $r + f = 0$, and then more gradually to relatively modest and uniform actual values of population density and consumption of energy.

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