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Nutritive quality of food in ecological systems

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With 1 table in the text

Abstract

The expression of net primary production in terms of dry matter, organic matter, carbon, or energy converts all units of plant production to an equivalent basis. However, net production differs in chemical composition and nutritive value depending upon species, plant age, and habitat. The nutritive quality of net primary production is very important in determining the efficiency of food utilization by herbivores. Nutrient content is equally important in determining the rate of decomposition of organic residues. Carnivores consume food of high nutrient content, especially with respect to protein, and adequate nutrition for these animals is likely determined by the amount of food consumption rather than by nutritive quality. Omnivores and detritivores fall somewhere between carnivores and herbivores with respect to the importance of food quality in regulating their growth and numbers in natural systems.

The use of energy flow or transfer in ecosystem analysis is a gross oversimplification of the relationships between organisms and their food. Energy utilization by consumers is regulated by nutritive quality of the food and all other factors regulating population sizes.

Introduction

The trophic-dynamic concept (LINDEMAN 1942) is a unifying approach to ecological study. Structure and function in ecosystems depend to a large extent upon the transfers of matter and energy through the various food webs. Food utilization data for individuals, populations, or trophic levels are converted to energy equivalents and the efficiencies of energy flow are calculated (ODUM 1959, KOZLOVSKY 1968, WELCH 1968). Energy budgets for ecosystems are prepared from estimates of energy flow at each trophic level (JUDAY 1940, LINDEMAN 1942, ODUM 1957, TEAL 1957, 1962, TILLY 1966).

Energy flow or transfer in ecological systems is an oversimplification of the relationships between organisms and their food. The capture of energy and formation of organic matter by primary producers are generally regulated by resources. The utilization of net primary production within the food webs of the system is determined by the quality of the net primary production (BOYD 1970 a, 1971) and other ecological factors regulating the numbers and growth of consumer and decomposer organisms. Energy

budgets simply describe the utilization of energy within an ecosystem. Energy utilization is regulated by the complex dynamics of physical, chemical and biological processes that operate in ecosystems. The term "bioactivity" (OHLE 1956) was suggested to encompass these relationships in aquatic systems. OHLE indicated that the processes involved in the uptake and release of energy (bioactivity) were so complex that they might never be completely unravelled.

This report is a nutritional consideration of certain aspects of energy relationships in ecosystems. Suggestions are given that may be valuable in understanding energy transfers. We are most familar with aquatic systems, particularly with respect to the macrophytic flora, so this discussion primarily concerns freshwater habitats. However, the ideas advanced can be extended to include any biosystem.

Primary production

Through the process of photosynthesis, green plants fix solar energy as chemical energy of organic compounds that are produced from inorganic carbon and water. A very small fraction (usually $< 3\,\%$) of the solar energy available for photosynthesis is actually converted into chemical energy by green plants. The total fixation of energy and organic matter is termed gross production. A portion of the gross production is expended by respiratory processes within the plant. The remaining plant biomass and chemical energy is the net production available to other trophic levels.

Regardless of the importance of the nutritive quality of net production, consideration must be given to factors that regulate the amount of production by different species. Even in systems containing species of high nutritive value, consumer populations may be limited by inadequate quantities of food.

Plant production is generally regulated by resources (HAIRSTON et al. 1960). The influence of temperature on production is well known in both aquatic and terrestrial habitats. Light is a very important factor in plant growth (BAINBRIDGE et al. 1966). In aquatic environments, transparency of the water and the depth at which plants communities are located affect the amount of light available for photosynthesis (SCHOMER 1934, MEYER & HERITAGE 1941, MEYER et al. 1943, WESTLAKE 1964, FOGG 1965, PELTIER & WELCH 1969, 1970). Carbon dioxide often limits the productivity of aquatic plants (KUENTZEL 1969, KING 1970). Inorganic nutrients other than carbon dioxide also limit the production of phytoplankton (GOLDMAN 1960, GOLDMAN & WETZEL 1963, POLISINI et al. 1970) and macrophytes (BOYD & HESS 1970, BOYD & WALLEY, unpublished). The response of terrestrial plants, particularly crop species, to nutrients is well documented. Light, tempera-

ture, available nutrients and various other ecological factors interact to determine the amount of net production of a species or community at a particular site.

Some species are inherently capable of higher production than others. For example, *Typha latifolia* (cattail) has tall, nearly vertical leaves and thereby exposes large surfaces for the utilization of solar energy (JERVIS 1969). Floating-leafed macrophytes such as *Nelumbo lutea* (spatterdock), *Brasenia schreberi* (water shield), and *Nymphaea odorata* (water lily) have leaves that float in essentially a single layer on the surface. This type of leaf morphology presents a minimum surface (one unit of photosynthetic surface for each unit of water surface) for light absorption. Standing crops of *T. latifolia* shoots may exceed 2,000 g/m^2 dry weight (MCNAUGHTON 1966) while floated-leafed species seldom exceed 300 g/m^2 (BOYD 1968, POLISINI & BOYD unpublished). The combined effects of morphology on the volume occupied by roots and shoots and the leaf surface available for light absorption are important in determining the potential of different species to produce dry matter and fix energy (LOOMIS & WILLIAMS 1969).

Species of aquatic macrophytes that occur at a particular site are determined by water depth, current, wave action, temperature, substrate characteristics, and water chemistry. Competitive interactions also occur between different species of macrophytes and between macrophytes and phytoplankton (see review by BOYD 1971). Dominant species of phytoplankton also vary between habitats due to various environmental factors. Seasonal changes in the dominant species of a given habitat are equally common (FOGG 1965). Species composition at terrestrial sites is also determined by environmental factors and biological interactions (OOSTING 1956).

In summary, the amount of plant production at a particular site is regulated by the influence of many environmental factors (physical, chemical, and biological) on the species that are present. Propagules of many species are available at most sites. Observed species composition is determined by factors that affect the biotic potential of the propagules.

Net production is usually expressed in terms of dry matter, organic matter, carbon, or energy equivalents of the organic matter per unit area. Quite often, standing crop rather than net production is reported for macrophytes. Such conventions are satisfactory for descriptive energetic studies of ecosystems or for comparative considerations of plant productivity where trophic-dynamic aspects are of no interest. Unfortunately, this approach neglects an important attribute of net production. Once sugars are produced in photosynthesis, these sugars and inorganic nutrients are used by the plant in the synthesis of an array of organic compounds. Chemical synthesis varies inherently between species and also differs within the same species at different sites or at different stages of maturity. The food value of plants

will obviously vary with chemical composition, so data on dry matter production or energy fixation by primary producers do not supply all of the information required for nutritional considerations of ecosystems. In the following discussion we will consider a few chemical constituents of plants in regard to nutritive value of net production. However, several other chemical components are probably as important as those included here.

Carbohydrates in plants are divided into two fractions, structural and non-structural carbohydrates (SMITH 1969). The structural carbohydrates include cellulose, hemicellulose, and lignin which are only utilized by animals that have hemicellulase and cellulase enzymes or in species capable of gastrointestinal fermentation of structural carbohydrates. Even for such animals, foods with high structural carbohydrate content (fiber) are less efficiently utilized than materials of lower fiber content (VAN SOEST & WINE 1967). Non-structural carbohydrates include sugars, starches, and fructosans which are readily utilized by all animals. VAN SOEST & WINE (1967) developed a technique for separating plant materials into cell-wall components (structural carbohydrate) and noncell-wall components. Application of this technique to samples of aquatic macrophytes demonstrated wide differences in the percentage of structural constituents in various species (POLISINI & BOYD, unpublished). Such differences are obviously important in determining the nutritive value of the plants in food webs.

Roughly 80 to 90 % of the nitrogen in plants is in the form of protein (LONG 1961, BOYD 1970 a). The total nitrogen content of plant material is a rough estimate of its total amino acid and protein content. Percentage nitrogen X 6.25 is used as an approximation of protein content. The amino acid composition of the protein of different species varies considerably (ALTSCHUL 1958), so the biological value of all plant proteins is not equal. However, for general purposes it is sufficient to use protein as estimated from nitrogen content as a measure of nutritive value. The total protein content of some species is consistently higher than that of other species (MORRISON 1961, BOYD 1968, 1970 a). Large intraspecific differences in protein content occur in samples of aquatic macrophytes from different sites (GERLOFF & KROMBHOLTZ 1966, BOYD 1969 a, b, BOYD & HESS 1970, BOYD & WALLEY, unpublished). For example, the protein content of *Typha latifolia* at 30 sites ranged from 5.4 to 13.2 % dry wt. (BOYD & HESS 1970), while the protein levels in *Saururus cernuus* varied from 9.1 to 16.1 % (BOYD & WALLEY, unpublished). Protein concentrations in leaves decline as the growing season progresses (LONG 1961, BOYD 1969 a, 1970 b, FEENY 1970).

The inorganic nutrient composition of different species of plants varies greatly (GERLOFF et al., 1964, BOYD & LAWRENCE 1966, BOYD 1970 c). Interspecific variation in the concentrations of various inorganic nutrients may occur in species within the same plant community. Differences in the in-

organic nutrient content of the same species from different sites or at different stages of maturity frequently occur.

Many plants contain compounds that are toxic to herbivores or render the plants unpalatable. Tannins are toxic to some herbivores (FEENY 1970). These polyphenol compounds also inhibit the digestibility of plant proteins (FEENY 1969, 1970). The effects of oak leaf tannins on the feeding of winter moth caterpillars is very striking (FEENY 1970). Tannin concentrations vary greatly between species of aquatic macrophytes (BOYD 1968), some species having more than 10 % of the dry weight as tannins. FENNY & BOSTOCK (1968) and FEENY (1970) showed that concentrations of tannins in oak leaves increase as the growing season progresses.

The chemical composition of individual plants obviously differs greatly between organs. Leaves are generally higher in protein and nonstructural carbohydrates than stems or petioles. Stems contain larger amounts of structural carbohydrates. Roots and rhizomes often contain large percentages of nonstructural carbohydrates, but comparatively small amounts of protein. Seeds are frequently high in fats, nonstructural carbohydrates and protein. Animals generally feed selectively on plant parts. For example, some feed on seeds, others on succulent young leaves, and some insects are specialized to feed upon phloem sap. These feeding habits are probably a response to nutritive quality. Total net production is of little value in estimating the quantity of food available to various organisms.

Variation in the total energy content of aquatic macrophytes with respect to species, site, and stage of maturity is much less than the variation in concentrations of inorganic nutrients, protein, and nonstructural carbohydrate (BOYD 1968, 1969 a, b, 1970 a). The caloric values of terrestrial vegetation are also fairly constant (Golley 1961). The constancy of caloric values is especially evident when results are reported on an ash-free basis. The caloric content of plant tissue is dependent upon its chemical composition. The average caloric values of protein, fat, and carbohydrate are 5.50, 9.30, and 4.10 kcal/g, respectively (MORWITZ 1968). Despite wide variations in composition of different materials, amounts of chemical constituents of differing caloric value approach a relatively constant ratio so that most plant materials have a caloric content around 4.0 to 4.2 kcal/g dry weight.

Only energy that is in the form of digestible nutrients is available to organisms feeding on plants. Data on the total caloric content of vegetation supplies no information on the nutritive value of the material. Regrettably, there can be no simple separation of the energy content of ecological materials into available and nonavailable fractions. Different organisms differ in abilities to digest various chemical components. However, for general ecological purposes, the determination of protein (total nitrogen

Table 1. Quantities of selected chemical substances and caloric contents of several species of aquatic macrophytes. Values for all constituents except tannins were obtained for samples from a single lake and should be subject to a minimum of between site variation.

Species	% Dry Weight						
	Protein[a]	Non-Cell Wall Constituents[b]	Tannins[c]	Ash[d]	Phosphorus[e]	Potassium[e]	Caloric Content (Kcal/gdry wt)[f]
Typha latifolia	4.0*	34.7	2.1	7.5	0.14	2.65	4.26
Hydrotrida carolinensis	10.5*	60.6	2.5	—	—	—	4.06
Brasenia schreberi	10.9*	70.4	1[illegible].8	7.6	0.14	0.99	4.03
Utricularia inflata	11.4*	59.3	—	14.0	0.12	1.98	4.02
Nelumbo lutea	12.1*	56.9	9.2	8.8	0.19	2.27	4.23
Myriophyllum heterophyllum	13.5*	63.0	3.2	12.2	0.16	1.25	3.96
Eleocharis quadrangulata	11.8**	44.1	—	—	—	—	—
E. acicularis	14.1*	—	2.0	11.2	0.24	2.86	4.26
Najas guadalupensis	14.4*	—	1.4	12.8	0.15	3.49	3.92
Nymphaea odorata	14.6*	58.1	15.0	8.1	0.18	1.28	4.18
Ceratophyllum demersum	17.1*	53.1	1.9	14.9	0.26	4.01	3.91
Nuphar advena	21.6*	68.5	6.5	10.6	0.40	1.88	4.32
Scirpus validus	5.8**	27.3	—	—	—	—	—
S. americanus	7.6**	37.0	—	—	—	—	—
Orontium aquaticum	21.2**	75.7	—	—	—	—	—
Juncus effusus	7.8**	27.9	—	—	—	—	—
Potederia cordata	8.8**	46.5	—	—	—	—	—

[a] Boyd, 1970 a; Polisini & Boyd, unpublished.
[b] Polisini & Boyd, unpublished.
[c] Boyd, 1968.
[d] Boyd, unpublished.
[e] Boyd, 1970 c.
[f] Boyd, 1970 a.
* True protein — sum of amino acids.
** Crude protein — nitrogen × 6.25.

X 6.25) and the amount of noncell-wall material (VAN SOEST & WINE 1967) should supply valuable information on the quality of net production.

For many purposes, primary productivity should be considered as two different and possibly unrelated processes. The first process involves the production of sugars and fixation of energy in photosynthesis. The second process, which we will designate as biochemical synthesis, determines the types and quantities of organic compounds produced from the sugars. The quality of net production and subsequently the efficiency of its utilization within the food web is determined by biochemical synthesis and inorganic nutrient accumulation by the plant. Chemical quality of net production is regulated by the genetic constitution of the species, but is also influenced by environmental conditions. Thus, a given plant population may contain a large quantity of dry matter and fixed chemical energy, but due to its chemical composition, be of little value as a food.

Some idea of the magnitude of interspecific variation in various chemical constituents of aquatic macrophytes can be obtained from Table 1. These data also emphasize the relative constancy of caloric values as compared with the wide variation in chemical components.

Consmer efficiencies

The energy budget of an animal was represented by WELCH (1968) according to the equation $I = G + R + E$ (I = ingestion, G = growth, R = respiration, and E = egestion). This equation could also represent the energy budget of a particular trophic level. Assimilation is the sum of growth and respiration, so the assimilation efficiency is A/I. The net growth efficiency is G/A. Growth as presented above is equivalent to the net production (NP) of KOZLOVSKY (1968) and represents the accumulation of energy by an animal, a population or a trophic level.

Such an energy budget is obtained by determination of the partitioning of the ingestion (dry matter) within the system under consideration and assigning energy equivalents to the different components. This is strictly a nutritional consideration. The magnitude of A/I is dependent upon the digestibility of the food (1). The growth efficiency (G/A) is determined by the efficiency with which materials absorbed through the gut (the assimilation of KOZLOVSKY 1968) is converted to biomass. WELCH (1968) considered growth to equal assimilation minus respiration. However, the efficiency with which material absorbed through the gut can be used for growth will vary with the composition of the food. This is particularly significant from the standpoint of the food supplying the nutritional requirements of an animal. An animal could obtain adequate digestible calories in its diet and still suffer from malnutrition due to the shortage of a specific nutrient in the diet. The

aquisition of sufficient protein in the diet will likely insure that a herbivore obtains adequate quantities of other nutrients. Plant parts that contain large amounts of protein are usually relatively rich in other nutrients. Furthermore, a herbivore feeding on low protein material must process a larger quantity of material to meet protein requirements and will thereby obtain adequate amounts of other nutrients.

Based on the studies of metabolism in man, it is apparent that after a meal is ingested the metabolic rate increases (GUYTON 1966). This increase is believed to be the result of processes involved in digestion, absorption, and storage of food in the body. The different classes of foodstuffs affect the metabolic rate to different degrees. Dietary protein generally causes a 30 percent increase in metabolism while fats and carbohydrates generally cause only a 4 percent increase (GUYTON 1966). The much greater specific dynamic action of proteins is thought to be the result of the greater number of energy releasing reactions which occur during digestion, absorption, and assimilation of proteins as compared to fats and carbohydrates (GUYTON 1966). Although these studies are based primarly on man, the principle probably holds for other animals as well since biochemical pathways for processing food are similar in most animals.

The efficiency with which an animal utilizes its dietary intake is obviously related to the composition of the food. Strict carnivores consume food which consist largely of protein so they must use more energy to process their food than herbivores which consume food of comparatively low protein content. WELCH (1968) observed that net growth efficiency was generally slightly higher for aquatic herbivores than for carnivores. It seems likely that the higher metabolic cost for assimilation of protein is the factor responsible for his observed separation of herbivores and carnivores. WELCH (1968) also noted that for the same organisms the assimilation efficiencies and gross growth efficiencies (G/I) were higher for carnivores than for aquatic herbivores. This evidence indicates an obvious nutritional difference between carnivores and herbivores. Carnivores are able to digest and absorb a higher percentage of their dietary intake but at a higher metabolic cost. In contrast, herbivores meet their dietary needs by taking in larger quantities of less digestable food. With respect to food requirements, carnivores are more limited by their ability to catch prey than on its nutritive value while herbivores are more limited by the nutritive value of the vegetation they eat. Omnivores occupy a position somewhere between herbivores and carnivores and obtain much of their protein requirements from animal tissue and much of their energy requirements from plant tissue.

The relative importance of various foodstuffs is indicated by nutritional studies of channel catfish, *Ictalurus punctatus*. DUPREE and SNEED (1966) fed catfish fingerlings a diet containing different levels of protein ranging

from 12 to 52 % (dry weight) but with caloric content constant. They found that weight gain increased with increasing levels of protein to about 40 %. Above that level weight gain decreased with increasing protein (presumably due to the metabolic cost of processing the protein). NAIL (1962) found that carbohydrate in the diet increased the utilization of dietary protein for growth and calculated that 0.23 g of carbohydrate fed per hundred grams of catfish would spare 0.05 g of protein. DUPREE (1969) found that small amounts of fat in the diet would also spare protein. However, increases in the amounts of carbohydrate and fats above 25 % carbohydrate and 14 % fat caused decreased growth (DUPREE and SNEED 1966). It should be pointed out that no growth occurred at the lowest protein levels and that the growth effects of dietary carbohydrate and fat require that adequate protein be in the diet (DUPREE and SNEED 1966). Consequently the level of protein seems to be the most important aspect of the nutritional value of the food.

Herbivores seldom consume all of the vegetation available to them. However, as pointed out by FEENY (1970), this cannot be construed to mean that herbivores are not food limited since much of the net production may not represent utilizable food. Plant communities composed of species with high nutritive values usually have larger herbivore populations than communities composed of plants of low nutrient content. Food crops have larger insect populations than pine forest. Dense populations of *Typha latifolia* are relatively indigestible and seldom grazed by herbivores. Floating-leafed macrophytes such as *Nelumbo lutea* and *Brasenia schreberi* have low standing crops but high nutritive quality and are heavily grazed by herbivores. Communities composed of many as compared to one or a few primary producer species have a greater diversity of nutrients and would be expected to contain a more diverse fauna. Consequently, energy budgets of ecosystems appear to be predetermined to a large extent by the quality of the net production and not necessarily related to energy as estimated by conventional calorimetry.

The effect of nutrient content, particularly nitrogen, on the decomposition of organic residues is well documented. Materials with high carbon and low nitrogen values are degraded by microbial organisms at a slower rate than residues with higher nitrogen contents (ALEXANDER 1961). Energy content as measured by bomb calorimetry is not related to the availability of organic residues to microbial populations. Admittedly, microbial species capable of degrading most organic residues are abundant in an ecosystem. However, if the rate of decomposition of a particular residue is slow in aquatic environments, the residue has a greater chance of being buried in sediments and thereby lost from the system.

Microbial biomass associated with decomposing detritus often increases its nitrogen (protein) content thereby improving the food quality (ODUM &

DE LA CRUZ 1967; KAUSHIK & HYNES 1968). Plants containing large quantities of structural carbohydrate (e. g. marsh plants) are converted into detritus of high food quality. The initial quality of net production may therefore be less important to detritivores than to herbivores.

The ecological efficiency of a population or trophic level is the fraction of energy ingested by the population or trophic level that is ultimately passed to another trophic level (SLOBODKIN 1960, 1962; MACFADYEN 1963; TURNER 1970). The efficiency with which energy ingested by a particular level of ecological organization is converted into the biomass of that particular consumer level (net secondary production) was discussed above. This secondary production will also enter food webs. Its nutrient content will be determined by ecological and genetic relationships. For example, some algal biomass is converted into herbivorous fish in aquatic ecosystems. The chemical composition of fish flesh will vary with species, stage of maturity, and environmental factors (PEARSE 1925; LAWRENCE 1968). However, there is much less variation in the nutritive quality of animals, especially vertebrates, than is observed in plants (BOYDS & GOODYEAR 1971). The nutritive quality, especially protein quality, of animals is obviously much higher than that of plants. Therefore, calorimetry is more suitable in estimating the digestible energy content of animal plant materials.

Ecological efficiencies are determined by food quality, physical and chemical properties of the environment that influence metabolism, physiological traits of organisms, and biological interactions between species. As OHLE (1956) recognized in his concept of bioactivity, all life processes are involved in energy transformations. The energy flow concept as traditionally visualized by ecologists is a oversimplification of energy relationships in ecosystems. The utilization of energy in ecosystems involves the collective nutrition of all component species. In essence, we are dealing with physiological and biochemical phenomena regulating the production and utilization of food as well as the complexity of factors not related to food that are also instrumental in determining the numbers, growth, and species composition of organisms in ecosystems.

We concur with OHLE that energy relationships in ecosystems are overwhelmingly complex and will likely nevere be entirely elucidated. However, much can be learned by the application of nutritional and biochemical techniques and concepts in trophic-dynamic ecology. Traditional energy flow considerations are so descriptive that they allow almost no insight into the biochemical and nutritional dynamics of ecological systems.

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Summary

The quantity of net primary production in ecosystems is regulated by the influence of many environmental factors (physical, chemical, and biological) on the species which occur in the system. Net production is usually expressed in terms of dry matter, organic matter, carbon, or energy per unit area. Unfortunately, this approach neglects the nutritive value of the net production. The nutritive value of plants differs greatly with species, stage of maturity, and site. Even different parts of the same plant often differ in nutritive quality. These differences in quality regulate the efficiency with which the plants can be utilized by herbivores. Only energy in the form of digestible nutrients is available to organisms feeding on plants, so caloric analyses of vegetation have little nutritional significance. However, valuable information on the nutritive value of vegetation can be obtained from protein analyses and the use of the neutral detergent procedure to estimate digestibility. Some plants of high nutritive value may be toxic or unpalatable to most organisms.

Nutrient content, particularly nitrogen, is important in determining the rate of decomposition of organic residues by microbial populations. Microbial activity frequently enhances the food quality of detritus.

Carnivores consume food of high nutrient content, especially with regards to protein, and adequate nutrition for these animals is likely determined by the amount of food consumed rather than by nutritive quality. Omnivores and detritivores probably fail somewhere between carnivores and herbivores with respect to the importance of food quality in regulating their growth in natural systems.

The energy flow concept as traditionally visualized by ecologists oversimplifies energy relationships in ecological systems. The utilization of energy in ecosystems involves the collective nutrition of all component species. We are dealing with physiological and biochemical phenomena regulating the production and utilization of food as well as the complexity of factors not related to food that are also instrumental in determining the numbers, growth, and species composition of organisms in ecosystems.

Zusammenfassung

Die Größe der Primärproduktion wird in Ökosystemen durch viele Umgebungseinwirkungen (physikalische, chemische und biologische) auf die Organismenarten beeinflußt. Die Nettoproduktion wird gewöhnlich durch Einheiten der Trockensubstanz, der organischen Substanz, von Kohlenstoff oder durch Energiewerte je Oberflächeneinheit in Äquivalenten ausgedrückt. Jedoch wird auf diese Weise der Nahrungswert der Nettoprodukte vernachlässigt. Der Nahrungswert der Pflanzen unterscheidet sich stark von Art zu Art und ändert sich mit dem Alter der Zellen. Sogar verschiedene Teile ein und derselben Pflanze weisen unterschiedlichen Nahrungswert auf. Diese Qualitätsunterschiede regulieren die Ausnutzbarkeit der Pflanzen für herbivore Tiere. Allein die Energie in Form verdaulicher Nahrung steht den Organismen zur Verfügung, die sich von Pflanzen ernähren, so daß Kalorienanalysen der Vegetation nur wenig aussagen über den Nahrungswert der Stoffe.

Andererseits kann man wertvolle Aussagen über den Nahrungswert der Vegetation durch Proteinanalysen erlangen. Einige Pflanzen von hohem Nahrungswert können für die meisten Organismen toxisch oder unaufnehmbar sein.

Der Nährstoffgehalt, insbesondere der an Stickstoff, ist für die Abbaurate organischer Substanzen durch Mikroorganismen wichtig. Durch mikrobielle Umsetzungen kann die Nahrungsqualität von Detritus häufig vergrößert werden.

Carnivore Tiere ernähren sich vor allem von Stoffen mit großem Nährwert, insbesondere im Hinblick auf Protein. Omnivore und detritovore Organismen fallen hinsichtlich der Bedeutung der Nahrungsqualität für die Regulierung ihres Wachstums in natürlichen Biosystemen graduell wahrscheinlich zwischen carnivore und herbivore Tiere.

Die Konzeption des Energieflusses, wie sie traditionell von Ökologen angenommen worden ist, stellt eine zu starke Vereinfachung der Energiebeziehungen in Ökosystemen dar. Die Ausnutzung der Energie in solchen Systemen schließt die gleichmäßige und gleichartige Ernährung aller vorhandenen Arten ein. Aber wir haben es mit physiologischen und biochemischen Erscheinungen zu tun, die die Produktion und Nahrungsausnutzung sowohl wie jene Faktorenkomplexe regulieren, die keine direkten Beziehungen zur Nahrung haben, aber dennoch wesentlich auf die Entwicklung der Zahl und das Wachstum und die Artenzusammensetzung der Organismen in Ökosystemen einwirken.

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