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Workshop agroecology

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

1984
pages 77-94

PRIMARY PRODUCTION IN AGROECOSYSTEMS

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Key Words: Agroecology, Primary Production, Soil Organic Matter.

ABSTRACT

The primary purpose of this paper is to compare data on the primary net production of various crop, forest and grassland ecosystems of the north temperate zone. These data suggest that net production is approximately the same for all types of ecosystems, if sufficient water for growth is available. An analysis of factors controlling production showed that the length of the growing season was of prime importance, as was adequate water. Fertilizers did not have a strong effect on net primary production, although yield is strongly related to fertilization. In the agroecosystems that have been studied intensively at Poznan, Poland, it has been shown that change in soil organic matter is of special importance in maintaining productivity. Management to control humus levels in soil involves the soil biota, inputs of organic matter through manure and green manure, control of erosion, and other factors.

RESUMEN

El propósito principal del presente informe es el de comparar datos sobre la producción primaria neta de diferentes ecosistemas de cultivos, bosque y pastos de la zona templada norte. Estos datos, sugieren que la producción neta es aproximadamente igual para todos los tipos de ecosistemas, si existe suficiente agua disponible para el crecimiento. Un análisis de factores controladores de la producción demostró que la duración de la estación de crecimiento era de gran importancia, al igual que lo era una cantidad adecuada de agua. Los fertilizantes no tenían un efecto importante sobre la producción primaria neta, aunque la producción estaba muy relacionada con la fertilización. En los agroecosistemas, que se han estudiado con mayor profundidad en Poznan, Polonia, se ha demostrado que los cambios en la materia orgánica del suelo son de especial importancia para el mantenimiento de la productividad. El manejo para controlar los niveles de humus del suelo, implica un control de los seres vivos del suelo, de los inputs de materia orgánica en abono y abono verde, un control de la erosión, y otros factores.

THE ECOSYSTEM CONTEXT OF AGRICULTURAL PRODUCTION

Agricultural activity focuses on yield, being part of the total net primary production, which is the plant material produced due to photosynthetic plant activity. Because of the immunity of basic photosynthetic processes to man's influence up to date, the strategy of agriculture is to increase the proportion of primary production which is used by man by manipulation of subsidy energy used for fertilizers, pest control agents, agrotechnology, breeding of more yield-productive kinds of cultivated plants and domesticated animals, changes in microclimatic conditions and so on.

It should be emphasized that the achievements of modern agriculture sprang from channeling the ecosystem's energy and nutrient fluxes into products useful for man. Thus, from the ecological point of view agricultural activity is connected with the change of the functional pattern of the ecosystem to magnify goals needed by man, but not with an expansion of the interception of solar energy by the biota. The utilisation of solar energy by the vegetation estimated for long periods, like the total vegetative period or a year, is very low, and in the majority of studied cases lies below 1 %. Under favourable conditions the energetic efficiency of primary production does not exceed 2 % (e. g., Iwaki, 1974; Nichiporovich, 1979; Wójcik, 1979; Lykowski *et al.,* 1980).

Shuffling the energy flow within the biota in ecosystems to maximize the productivity of desirable products is accompanied by the simplification of agroecosystem structure and by a decrease in efficiency of solar energy conversion between the remaining components (Ryszkowski, 1979 a). In addition, man has to provide the energy subsidy for maintaining the desired, simplified structure of agroecosystems, as well as for preventing development of natural succession processes and so on. Thus, theoretically, one can expect two sources of higher energy expenditure in agroecosystems: one due to lower efficiency of energy conversion between trophic levels and the second connected with added energy by man to achieve specific goals.

New technologies, energy and matter inputs and economic incentives were the main reasons for the global increase in yields, especially of the major cereal crops, since the World. War II. This increase, without precedent in agricultural histoy, in many countries began to level off by the beginning of the 1970's and further increase of crop production has been achieved largely by bringing more land under cultivation. The application of fertilizers, pesticides, herbicides and other means of high-energy crop production technology was developed without sound ecosystem knowledge, mainly by detection of positive correlations between inputs (factors of production) and outputs (yields). Lack of understanding of component ecosystem processes, which tie inputs to outputs, is probably the main obstacle to further big yield increases. It seems, therefore, that further energy intensification alone would not produce spectacular effects in developed countries.

The other reason for development of sound agroecosystem knowledge stems from recognition that the agricultural landscape serves as an unintended sink for many industrial contaminants, such as sulphur, which have a potential impact on agricultural productivity (Reinert *et al.,* 1975; Bialobok, 1979). The heavy applications of chemical fertilizers used by modern agriculture in many countries also have led to upsets in agricultural landscapes. Examples are the eutrophication of aquatic ecosystems and the development of hazardous levels of nitrate in the water supplies. These problems could be solved only on the basis of engineering of matter cycles in the agricultural landscape.

The agroecosystem approach allows us to make a rigorous examination of components within the agroecosystem such as the soil, animals, crop, livestock, and so forth, and their interactions, and to characterize in this context inputs and outputs to the system. Such a wholistic approach to the agricultural system permits us to evaluate the perspective of crop improvement enterprises.

The pattern of organic matter production and accumulation is a result of generation and removal processes which in many cases are controlled by secondary productivity of heterotrophs, that is, by the microbe and animal components of agroecosystems. On the other hand, attributes of soil, especially soil organic matter, and vegetational cover have been shown to operate as key regulators of nutrient pools as well as the control mechanism of water cycling within an agricultural landscape. Thus, primary production processes provide not only food and fiber for man but also should ensure regeneration of humus, provide energy for heterotrophs living in the system, and control wind or water erosion processes and so on. The integration of various nutrient cycles through soil organic matter is another important functional characteristic of ecosystems.

Despite the extensive number of studies on nutrient-yield relationships the patterns of matter cycling within agroecosystems are still insufficiently understood. There are indications that agroecosystems have more open cycles of mineral circulation than other terrestrial ecosystems (SIDA, 1972; Ryszkowski, 1974, 1979 b; Ursic and Dendy, 1965; Frissel, 1977; Krebs and Golley, 1977; Borowiec *et al.,* 1978). Despite the incompleteness of present information the following preliminary functional characteristic can serve for comparative evaluation of agroecosystems with other terrestrial ecosystems. Cultivated fields are ecosystems maintained by human intervention at an early stage of succession with simple structure, little potential for modifying the effect of climatic factors and open cycles of mineral circulation. In these ecosystems, the cost of maintaining the stability of the system is borne by man, who influences practically all ecosystem processes (Ryszkowski, 1975). From a theoretical as well as a practical point of view, the understanding of primary production processes has the utmost importance for the future strategy of agriculture.

In order to examine the changes in patterns of primary production evoked by agriculture, agroecosystems were compared with natural grassland and forest ecosystems. Analyses carried out in this paper, are restricted to the north temperate zone.

PRIMARY PRODUCTION RATES OF TERRESTRIAL ECOSYSTEMS OF THE TEMPERATE ZONE

The great achievements of the International Biological Programme resulted in several synthesis volumes providing an overview of productivity processes at the scale of the world. Assuming a broad definition of the north temperate terrestrial zone as the land situated between 30° and 60° N latitude, one can find 21 estimates of total annual primary net production in grasslands (Coupland, 1979) and 19 estimates in forest ecosystems (De Angelis *et al.,* 1981). French *et al.* (1979) provide information on primary production estimates in agroecosystems. This last set of data was supplemented by new published data as well as by unpublished estimates evaluated already in the Department of Agrobiology and Forestry, Poznan, Poland. To date, it was possible to gather 75 estimates in various agroecosystems from the north temperate zone in America, Asia and Europe.

Methods of net primary production estimation vary between the types of ecosystems studied as well as within each kind of ecosystem. The most frequently used methods in agroecosystems and grasslands were: a) peak standing crop, and b) summation of biomass increases of above and below-ground parts of plants, including or not including fall of above-ground parts of plants between sampling dates and consumption by herbivores. In estimates carried out in the Department of Agrobiology and Forestry, Poznan, Poland (DAF), besides estimates of above and below-ground production of main crops and weeds, consumption by herbivores and fall of plant parts between samples, were included also estimates of moss production, self-sown plants (e.g., rye) sprouting from discarded seeds during harvest as well as regrowth of weeds. If after-crops or fore-crops were raised additionally to main crops, their production during the year also was included in the annual estimates of a field production .

Estimates of forest productivity are most frequently made by one or another modification of the dimensional method based on direct measurements of sizes and weights of trees or bushes, synthesizing the obtained measurements into production estimates by "mean-tree" regressions between characteristics. For estimates of herb layer production the methods used in grasslands or agroecosystems are applied.

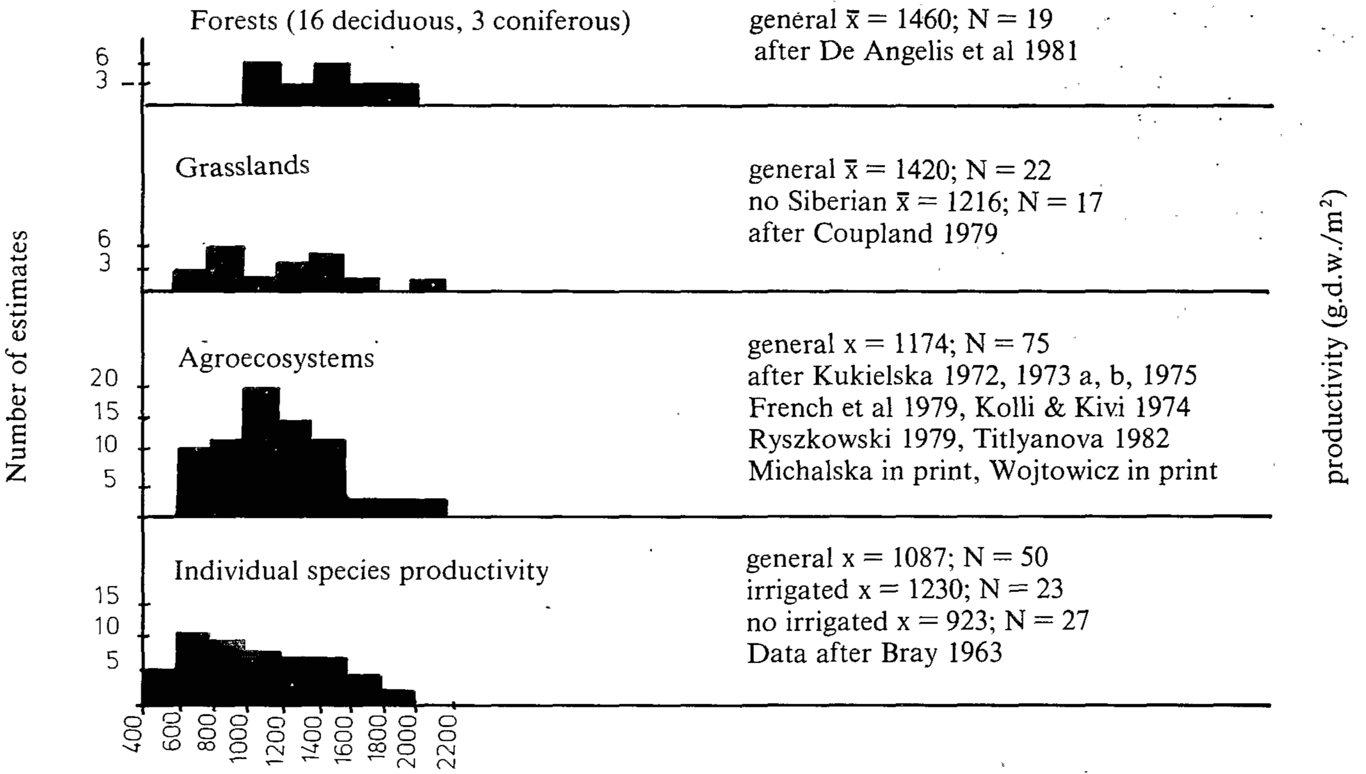
Estimates of primary production in the three basic types of terrestrial ecosystems do not include sloughed cells and exudates of roots, nor the algal production.

It is important to keep in mind the variability of the methods applied and the various accuracies achieved when analysis of results is carried out.

The average annual primary production in 19 studied forest ecosystems was estimated to be 1460 g.d.w.m^{-2} (Figure 1). In 19 estimates of total primary production presented in the IBP woodlands data set (De Angelis *et al.,* 1982) were 16 decidous and 3 coniferous forests. The mean for deciduous forests is 1438 g.d.w.m^{-2}, while the average estimate for three coniferous forests is 1580 g.d.w.m^{-2}. The variability of estimates within both subsets of data encompass the difference between mean values for those two types of forest ecosystems and, therefore, in the following analysis the general mean for both types of forests is used.

The average annual grassland primary production evaluated on the basis of 21 IBP estimates (Coupland, 1979) is 1420 g.d.w.m^{-2}. Very high estimates were obtained in two of five studied grassland ecosystems in Siberia. In a steppe ecosystem dominated by *Calamagrostis epigeios* and *Poa angustifolia* total production amounted to 3100 g.d.w.m^{-2} and in dry grassland dominated by *Festuca pseudovina* and *Artemisia pontica*

Figure 1. Distribution of annual primary productivity in diverse ecosystems of temperate zone.



the estimate reached 3470 g.d.w.m^{-2}. In both cases the high estimates of total production resulted from very high under-ground production being respectively, 86 % and 92 % of the total. In North America short grass prairie (e.g., Pawnee, Colorado), resembling physiognomically dry Siberian steppe, the estimates of annual primary production were four times lower and amounted to 740 g.d.w.m^{-2} The methods of estimations were completely different in the two sites. In Siberia, Titlyanova's (1977) estimates included evaluations of the fall of above and below-ground biomass between sampling dates calculated by difference balance equations. The high Siberia estimates were mainly due to this reason. If the five Siberian estimates are excluded from calculation of the general mean for grassland ecosystems, then the average value drops to 1216 g.d.w.m^{-2}. The difference between the general mean production rate in forest ecosystems (1460 g.d.w.m^{-2}) and grassland ecosystems without the Siberian estimates (1216 g.d.w.m^{-2}) is on the verge of statistical significancy ($t = 2.22$, $p = 0.0357$). A conclusion about the similarity between production rates in forest and grassland ecosystems depends on the arbitrary decision of the acceptation of confidence limits of $p = 0.01$ or $p = 0.05$.

The average annual primary production in agroecosystems was estimated to be 1174 g.d.w.m^{-2} (Figure 1). If the 32 estimates obtained by the staff of DAF in the Turew agricultural landscape are treated separately, then the mean annual primary production in agroecosystems of Western Poland is equal to 1347 g.d.w.m^{-2} and there is no statistically significant difference between the production rate in Turew agroecosystems and forest, as well as grasslands, irrespectively if the Siberian estimates are or are not included in calculation of the general mean. The average annual production estimated for 43 agroecosystems studied outside of Turew is equal to 1113 g.d.w.m^{-2}. The difference between the Turew data and that for the rest of the temperate zone is partly related to inclusion of after -and fore-crop production rates into the annual estimates obtained in Turew.

Bray (1963) presented estimates on annual production of above and below-ground parts of individual cultivated herbaceous species. The mean calculated for 50 estimates cited by Bray (1963) is 1087 g.d.w.m^{-2} (Figure 1). Some of the data presented by Bray (1963) were obtained in irrigated fields. Irrigation stimulates production and the average annual production of individual species is higher (1230 g.d.w.m^{-2}) than the production of species grown in unirrigated conditions (923 g.d.w.m^{-2}).

Iwaki (1974) presented results of studies on primary productivity carried out within the IBP Japanese project con "Maximum growth rate experiments". Climatic conditions of studied experimental agroecosystems were favourable and intensive cultivation was applied. The average estimate of annual production (wheat, barley, oat, rye, rape, sugar beet) in crops growing in the field at least 200 days was 1680 g.d.w.m^{-2}. This value is almost equal to production of Turew fields in which rye as fore-crop and potato as main crop were grown during one year (Table 1).

According to Iwaki (1974), the production of paddy rice during 115-130 days was estimated to be 1449-1830 g.d.w.m^{-2}. If two crops could be produced per year then probably higher values of annual primary production would be obtained.

The highest value of annual primary production obtained in the vicinity of Turew, Poland amounted to 2020 g.d.w.m^{-2} and was observed in an alfalfa plantation with sown-in oats growing under favourable climatic conditions.

Both the calculated means as well as the range of estimates of primary production are lower than estimates approximated by Loomis and Gerakis (1975) from recorded yields using an assumed ratio of crop to total net production.

On the other hand, the estimated values of net production in cultivated fields are higher than the values used in attempts to evaluate primary production on a world scale. Recently assumed values for cultivated lands are as follows: 650 g.m^{-2} year (Lieth, 1975; Whittaker and Likens, 1975; Golley, 1972) and 880 g.m^{-2} (Olson, 1970).

It can be concluded from the analysis that the average primary production in temperate agroecosystems could be lower than or similar to the average annual production of forests and grasslands which do not exist under conditions of water deficit.

To approach more precisely this problem deeper knowledge on the driving variables of the primary production is needed.

FACTORS INFLUENCING PRIMARY PRODUCTION RATE

Production in grasslands or forests is the result of plant photosynthetic activity during the entire vegetation season. Cultivated plants usually grow in shorter spans of time in agroecosystems because of applied crop rotation and harvest patterns, agrotechnology used and other factors which control the existence of plants in the field. Growth of cultivated plants is simultaneous and the sequence of developmental stages is highly

Table 1. Influence of the length of the growth period on primary production.

Crop	Growth period (months)	Number of estimates	Average production (g/m^2 year)	Locality, author
Potato	4.0	4	1128	Turew, Kukielska 1973 a, b, 1975
Rye	9.0	10	1328	Turew, Kukielska 1973a, 1975 Wójcik 1973, 1979
Rye as forecrop and potato as main crop	11.0	6	1637	Turew, Kukielska 1975 and unpublished data.
Barley	3.5	5	907	Tartu, Kolli & Kivi 1974.
Potato	4.0	5	832	Tartu, Kolli & Kivi 1974.
Rye	11.0	5	1133	Tartu, Kolli & Kivi 1974.

Table 2. Comparison of primary production in barley field and meadow steppe (calculated from data for 1973 of Kashkarova 1976, and Utekhin and Hoang Chung, 1976).

ecosystem	soil	production (g.d.w/m^2)	growth period (months)	peak root standing crop (g.d.w/m^2)	mean LAI (m^2/m^2)	biomass increase per month (g)
barley	chernozem	1228	3	349	3.05	409
steppe	chernozem	1752	5	1790	2.14	350

synchronized, which is in striking contrast to grasslands or forests. One could expect lower values of primary production when the existence of the plant cover in the field is shorter than where the time span of crop cover matches the vegetation season. This expectation was proved in studies on the effect of growing season length on increasing total production. When potatoes are cultivated only, plants exist in the field about four months and during the rest of year the field is fallow, or the soil is covered by sparse weeds, and lower net primary production is achieved than when a fore-crop of rye for cattle forage and main crop of potatoes are cultivated in one year and plant cover exists over 11 months (Table 1).

The same results are obtained when production is compared in plants having various spans of growth periods. By the same method the primary production was estimated in rye, barley and potato crops by Kolli and Kivi (1974). Under the climatic conditions of Estonia the winter rye is growing 11 months. Barley and potato cultivation grow 3.5 and 4 months,respectively, and their production is lower than the primary production of the rye agroecosystem (Table 1). The growth rate per month calculated on the basis of the entire span of existence in the field is much lower in winter rye than in spring plants. But the winter rye agroecosystem can take advantage of autumn solar radiation as well as spring solar radiation (e.g., appearance of early spring weeds). Potato or barley agroecosystems show higher average production rates per month than winter rye, but practically no plant cover exists during some suitable growth months both in spring and autumn. Thus, the growth rate per short span of time, e.g., per one day, or even one month, provides a poor basis for evaluation of the primary production rate for the entire vegetation period. This conclusion can be supported by comparison of the annual primary production in a barley agroecosystem cultivated side by side to the native meadow steppe, both growing in the same chernozem soil (Table 2). Barley's biomass increase rate per month is about

Table 3. Influence of soil moisture on richness of herbs in rye fields (Wójcik 1983).

Associations and subassociations	Average number of species	
	typical variant	wetter variant
Vicietum tetraspermae consolidetosum	27.0	38.0
typicum	25.5	35.2
sperguletosum	20.0	26.5
Papaveretum argemones	25.2	37.0
Teesdaleo-Arnoserdetum	14.0	35.0

17 % higher than rate observed in the meadow steppe vegetation. But plants in the steppe ecosystem grow much longer than barley and total primary production in the steppe is higher by about 43 % than the barley field production. The higher rate of growth per month in barley is due to a higher value of the leaf area indices (LAI).

As is well known, available water and temperature are main factors associated with increased net primary production. This relationship was recently shown in agroecosystems by Kaczmarczyk (1976). The soil moisture increase is related to increase of the species richness of the weed community existing in the rye agroecosystem (Table 3). It can be assumed that the most crucial point concerning the water-plant relationship is the problem of a good match in water supplies and the demand for increased transpiration during the intensive plant growth period. Thus, the amount of precipitation water during the plant intensive growth period could influence the annual primary production to a higher extent than the fall during the entire year. A significant correlation was found between the amount of rain fall in the time span from April to July and the total productivity of the rye ecosystem (Figure 2), while the correlation of the amount of rain fall in the period from October to July next year (the entire span of winter rye vegetation) and the rye field primary production is insignificant. The whole 1969 year in Turew was dry and the net primary production amounted to 1168 g.d.w.m^{-2}. The light, lessive soil of Turew has no great capacity to hold moisture and when the next year, as happened in 1970, also is characterized by a little bit higher amount of rain fall in the first half of year then the deficit of water is extended and primary production is decreased. This situation is documented by the first two points on Figure 2. Slightly higher rain fall in the April -July period did not result in an increase of the primary production rate because of accumulated drought.

Above differences in primary production of the individual cultivated species growing under irrigated and unirrigated conditions (Bray, 1963) also show the great importance of water for increase of the biomass productivity rate. The recent studies on heat balance of a plant cover carried out under field conditions also show the significant role played by water in productivity processes. The influx of solar energy to the field is the driving energetic input to all climatological and biological processes appearing in biosphere and atmosphere. The balance between the intercepted influx of global (direct and scattered) radiation and reradiated long wave energy called the radiation balance, measure the amount of intercepted energy by the ecosystem. The

Figure 2. Fall from April to July and productivity of rye ecosystem.

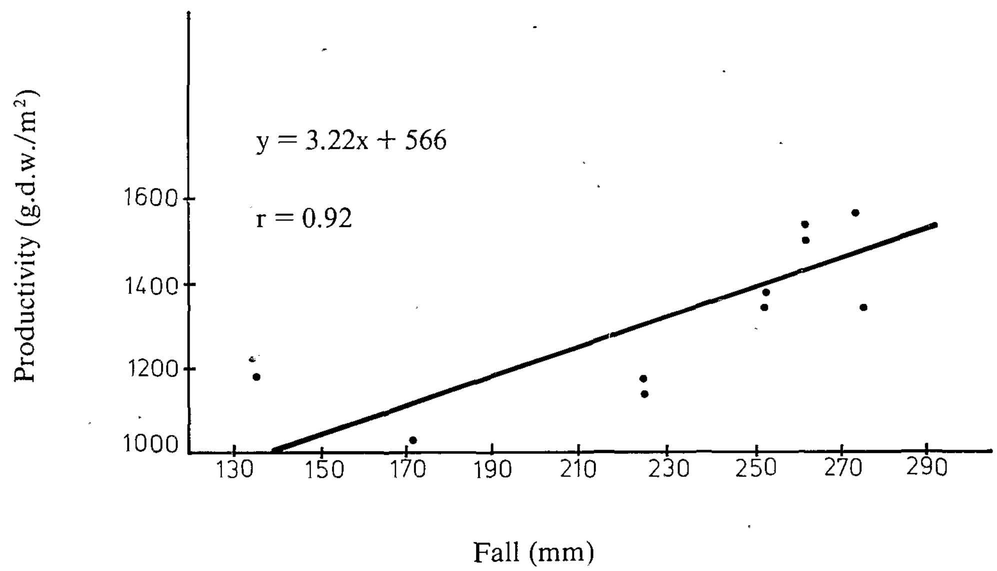


Table 4. Components of heat balance in alfalfa agroecosystem (MJ / m^2 / day). A. Kedziora (personal information).

Day	R	λE	C	G	Balance	Ratio of balance to R
25.05	2.6	-2.5	-1.1	+ 0.8	-0.2	-0.07
27.05	11.9	-6.9	-5.5	-1.0	-1.5	-0.13
29.06	13.0	-10.9	-3.4	-0.1	-1.4	-0.11
12.07	9.2	-5.8	-3.3	+ 0.8	+ 0.9	+ 0.09
16.08	11.6	-5.9	-5.1	-1.1	-0.5	-0.04

Energy used for: evapotranspiration (λE), heat exchange with soil (G), exchange of sensible heat with atmosphere (C).

Balance of radiation R (intercepted influx of global radiation minus radiated long waves energy) — used energy + lost energy.

Table 5. Influence of mineral fertilization on total primary production.

crop	dose (kg/ha)			production (g.d.w./m^2)	grain yield (g.d.w./m^2)	below ground production %	soil and author
	N	P	K				
winter* rye*	41 74	33 72	50 120	1536 1514	426 393	19 14	lessive, Kukielska 1975 and unpublished
winter* rye*	34 66	36 72	45 90	1344 1470	359 372	21 20	lessive, Kukielska 1975 and unpublished
spring barley	120 530	200 420	80 200	1215 1282	325 368	43 31	typical chernozem, Kashkarova 1976
spring wheat	0 45	0 290	0 0	1189 1205	294 271	27 30	podzolic chernozem, Titlyanova et al. 1982
spring wheat	0 180	0 0	0 0	912 1032	176 235	38 32	podzolic chernozem, Titlyanova et al. 1982

* Dose of fertilizer recalculated per active element

major part of the intercepted energy is usually spent to drive evaporation and transpiration processes. In the period of intensive plant growth, it was observed that the ratio of energy used in evapotranspiration processes surpasses the amount of intercepted energy (Lykowski *et al.*, 1980). In this situation the additional energy for evapotraspiration probably is brought by advection of heat from the adjacent fields or forests where the evaporation of water is not so intensive.

The recent studies of A. Kedziora (personal information) proved that situations of energetic deficit for evapotranspiration happen quite frequently under field conditions (Table 4). This finding shows that the water regime of agro-ecosystems has the utmost significance for productivity processes under field conditions.

An unexpected result from studies on primary production in agroecosystems is the finding that fertilizers have a rather small influence on total net primary production (Table 5). Everybody knows about the important influence of mineral fertilizers on yield increases and, therefore, there is no need to show supporting figures. Crops are selected to take better advantage of the chemicals provided by man. Cultivated fields in high - energy crop production technologies are regarded less and less as an ecosystem but as a site on which chemicals provided by man could be converted, with the use of solar energy, into a desired food or fiber. Chapin (1980) pointed out that crop species evolved from ruderal herbaceous plants growing in fertile habitats. Wild plants from the fertile habitats show a distinct growth rate, and less developed root systems than plants from infertile soils, which enable them to have rapid growth, high reactivity to mineral supplies and less economical use of minerals. From wild ruderal plants man selected varieties that were more responsive to fertilizers through production of desired yields, but not through increase of the entire plant biomass. For example, high-yield, dwarf varieties of wheats have less intensive root systems than less productive varieties. High grain production is compensated by less intensive root development. If this suggestion is correct, then increased yield obtained by application of mineral fertilizers is slightly reflected in increase of total net primary production. Thus, by the use of fertilizers, man changes the proportions of primary production to his advantage rather than changing the total amount of organic matter produced. This hypothesis is supported by the convergence of net primary production values observed in forests, grasslands and agroecosystems if proper correction for growth period is made.

Thus, analysis of factors influencing the net primary production in agroecosystems has shown that the length of the growth period is a very important factor. Any factor, which extends photosynthetic activity of plants will have a profound impact on the primary production rate.

The second in the rank of factors influencing net primary production is probably the water regime, especially the timing of water fall with plant growth periods, as well as the soil's ability to store moisture which partly can compensate for lack of water during rainless periods. Water storing capacity of soil is influenced by content of organic matter (humus) and mechanical composition of soils (texture). Thus, a higher content of humus as well as a higher precentage of very

Table 6. Relationship between soil texture and yields. (after Witek 1979).

Soil		Yields (t/ha)		
type	texture	winter	rye	oats
heavy	medium-heavy loam	4.8	4.0	4.3
	sandy loam	5.2	4.6	4.5
medium heavy	loess	4.7	4.5	4.4
	medium sand on loam	4.4	4.6	4.5
light	medium sand	3.3	3.8	3.5

Table 7. Type of soil and richness of herbaceous flora in agroecosystems (after Wójcik 1983).

Soil made of:	Average number of species in association
loose sand	12 - 15
medium sand	20 - 25
loam or clay	30 - 35

small particles (e.g., less than 2 μm in effective diameter) influences higher capacity of the soil to store water. Increased water storing capacity is one of the reasons why one can find correlation between soil texture and yield (Table 6). In agroecosystems situated on light soils the yield is usually poorer than in fields having medium heavy to heavy soil. Of course, this trend could be reversed in years characterised by high water fall.

Differences in methods used by various authors for evaluating net primary production prevent detection of a direct relationship between soil texture and productivity rate in agroecosystems. Taking into account the small influence of mineral fertilizers on total net primary production, one should not expect a direct relationship between soil texture and total net primary production. Nevertheless, on loam or clay soils many more species of weeds are observed than on loose sand (Table 7).

Kolli (1977) found that total above-ground annual production of the barley agroecosystem is lower in comparison to above ground production of a coniferous forest when comparisons were made in ecosystems situated on loamy soils. On sandy soils the opposite picture was obtained. But, because of the lack of under-ground production rate estimates, no inference can be made with respect to the total ecosystem productivity.

It seems that the relationships between mineral nutrients and soil texture with respect to yield are much stronger than the relationships between these factors and the total net production of agroecosystem.

COMPENSATION BETWEEN PARTIAL PRIMARY PRODUCTIVITY PROCESSES AND RELATIONSHIP BETWEEN TOTAL PRIMARY PRODUCTION AND YIELD

If there is a weak correlation between mineral nutrients and total net primary production, one should be able to find compensation processes between partial production rates of components of net primary production, resulting in greater stability of total net production in comparison to partial productivity processes. Thus in a situation when pests eliminate some cultivated plants, the better growth of weeds could result in some compensation of total production in place of the lost plant biomass. If this is true, then the variability of a compartment's production rate would be higher than the variability of the total net production values. Analysis of variability could be simply carried out by comparisons of variability coefficients (value of sample standard divided by the mean; G : $\overline{x}$) if large enough series of estimates were obtained by the same method of evaluation for the same crops. Five such series of estimates were analyzed (Table 8). In four out of five cases the variability of total production was the lowest. In all analyzed cases the variability of weeds productivity was the largest. In all cereal agroecosystems the variability of straw production was higher than the variability of total net production. Only in the case of barley, the productivity of grain showed lower variability than total primary production. In potato agroecosystems the production of tubers showed higher variability than net primary production. Thus, one can conclude that there are compensation processes between components of primary production resulting in the greater stability of total net primary production.

The other compensation process which could be shown to operate in primary production of agroecosystems is shoot elimination or death. Due to better moisture conditions or due to higher fertilization rates more sown grain can sprout. During the growth of the plant cover, the competition begins between plants and some of them are eliminated. Thus, biomass of eliminated plants contribute to the total primary production and the amount of biomass eliminated could be an expression of compensating processes between compartments of net primary produc-

Table 8. Variablity of productivity components.

Author	Kukielska in press			Koll and Kivi 1974									Kukielska in press		
Crop	rye			rye			barley			potato			potato		
statistics	$\bar{x}$ g.d.w./m²	%	$\sigma/\bar{x}$	$\bar{x}$ g.d.w./m²	%	$\sigma/\bar{x}$	$\bar{x}$ g.d.w./m²	%	$\sigma/\bar{x}$	$\bar{x}$ g.d.w./m²	%	$\sigma/\bar{x}$	$\bar{x}$ g.d.w./m²	%	$\sigma/\bar{x}$
grains or tubers	327	25	19.6	212	19	26.6	259	29	12.9	415	50	23.8	493	45	32.5
straw	609	46	16.8	398	35	24.6	198	22	31.3	—	—	—	—		
weed	33	2.4	69.3	25	2.2	104.0	6	0.7	117.0	5	6	32.0	231	22	91.0
Total production	1328	100	14.8	1133	100	10.1	907	100	19.3	832	100	20.7	1050	100	25.8
Number of estimates	10			5			5			5			10		

tion. The density of sprouting rye is about three times more variable than the density of rye plants in summer (Table 9). The higher the sprouting density, the lower the production of weeds, or the lower the production of surviving crop plants. At present we have not enough data to support this hypothesis but observations of Loomis and Gerakis (1975) have shown that in maize, when competition between densely growing young plants is strong then the plants produce no or very little grain.

Of course various crops show different intensity of plant elimination (Table 10). The rape (*Brassica napus*) loses during winter a substantial part of the above-ground production produced in autumn. This kind of elimination probably has small bearing on the above compensation process. But elimination in beet agroecosystems probably has important compensating meaning. In big, branchy plants, like potatoes, the elimination of even a few plants could have an impact on the realized total crop productivity

Table 9. Elimination of shoots in rye cultures (calculated from Kukielska's data).

Season	Shoot density per one m²									$\bar{x}$	$\sigma/\bar{x}$
spring	760	1294	715	873	589	1251	1365	674	732	884	0.34
summer	424	442	371	438	392	384	317	327	384	386	0.12

Table 10. Elimination of shoots in various crops (Wójtowicz in press).

Crop	Density (ind/m²) at time of		Elimination
	germination	harvesting	%
rape	265	69	74
beet	27.3	3.6	87
wheat	702	360	49
maize	8.1	7.4	8

(Table 11). Thus, grazing by herbivores like Colorado beetles (*Leptinotarsa decemlineata*) could have a real impact on total primary production in agroecosystems. The impact of herbivores on growth of cultivated plants is dependent on the timing of grazing activity with the phenology of plant growth. Thus for alfalfa, grazing in June - August by voles has a critical effect on the appearance of damage. For rape, the critical period is between December and April and for cereals between May and June (Ryszkowski, 1982; Truszkowski, 1982). Outside of these periods grazing has small influence, even if it is intensive because of the regenerative capacities of the plants or because the plants are too lignified to be eaten by voles.

The total primary production is correlated with yield, although a broad scatter of points is observed (Figure 3). Generally speaking there are arbitrary and objective reasons for the observed scatter. Which parts of plant productivity constitute the yield is up to man's will. For example, in the rye field the yield could consist of grain only or of grain and straw. Thus, the choice by the farmer of the plant parts which are removed from the field is determined by arbitrary decision and varies according to cultivated plant kind as well as the economical needs of his farm.

The objective reasons for the observed scatter in correlation of total net primary production and yield are: a) kind of plant cultivated (e.g., in winter rape plantations the loss, because of shedding almost all the above-ground autumn production, is much higher than in winter rye, which causes a different ratio of total net primary production and yield in these two crops); b) influence of various weather conditions which create differences in production of individual compartments of total net production. In situations when yield consists of a substantial part of primary production, e.g., grain and straw, the value of correlation is higher than when the smaller part of primary production is considered as the yield. Thus much higher correlation was found between total net production and grain plus straw removed from field by the farmer than between total net primary production and grain yields (Figure 4).

Table 11. Decrease of potato productivity due to plant elimination during the growth period.

Density (ind/m²) at time of:		Estimated production (g.d.w./m²)		
planting	harvesting	real	if no elimination	%
4	2.4	898	1476	164
4	3.7	1167	1236	106
4	2.5	1119	1415	126
4	2.6	596	941	158

Fig. 3. Relationship between proudctivity and yield in vicinity of Turew, Poland.

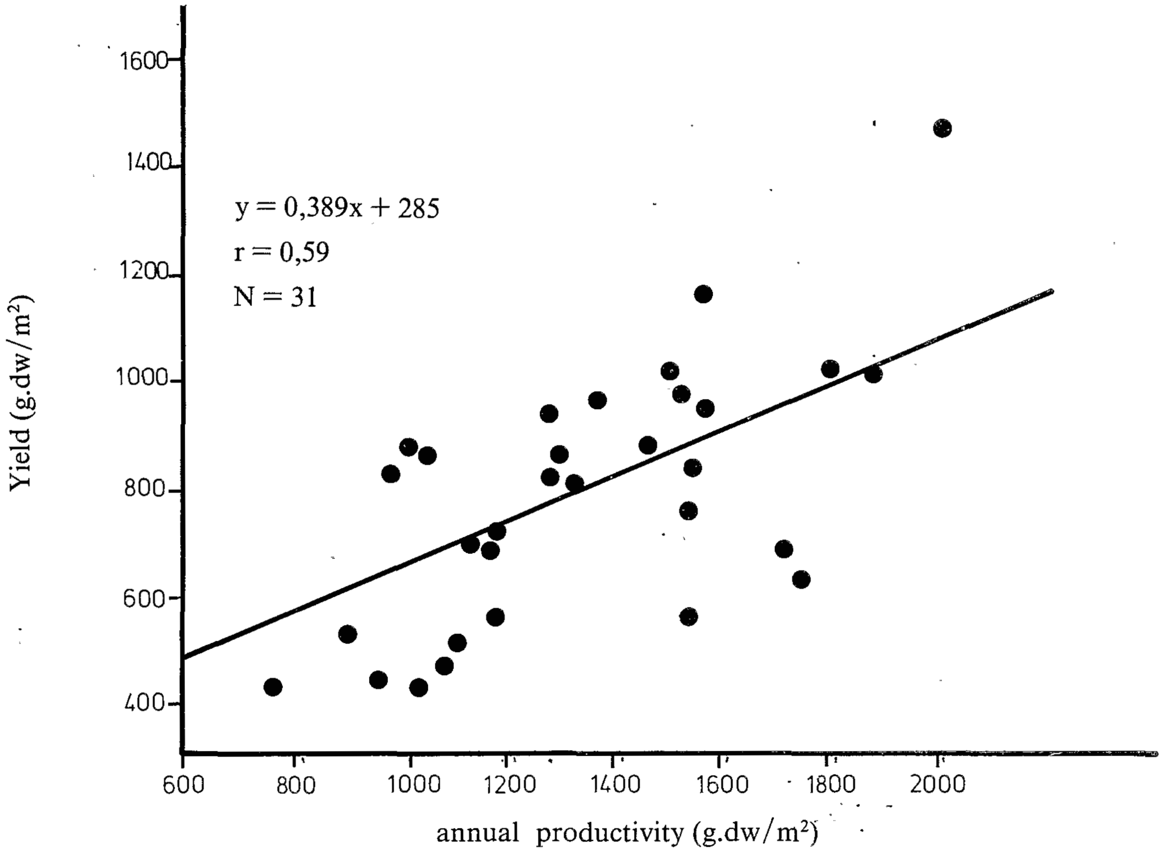
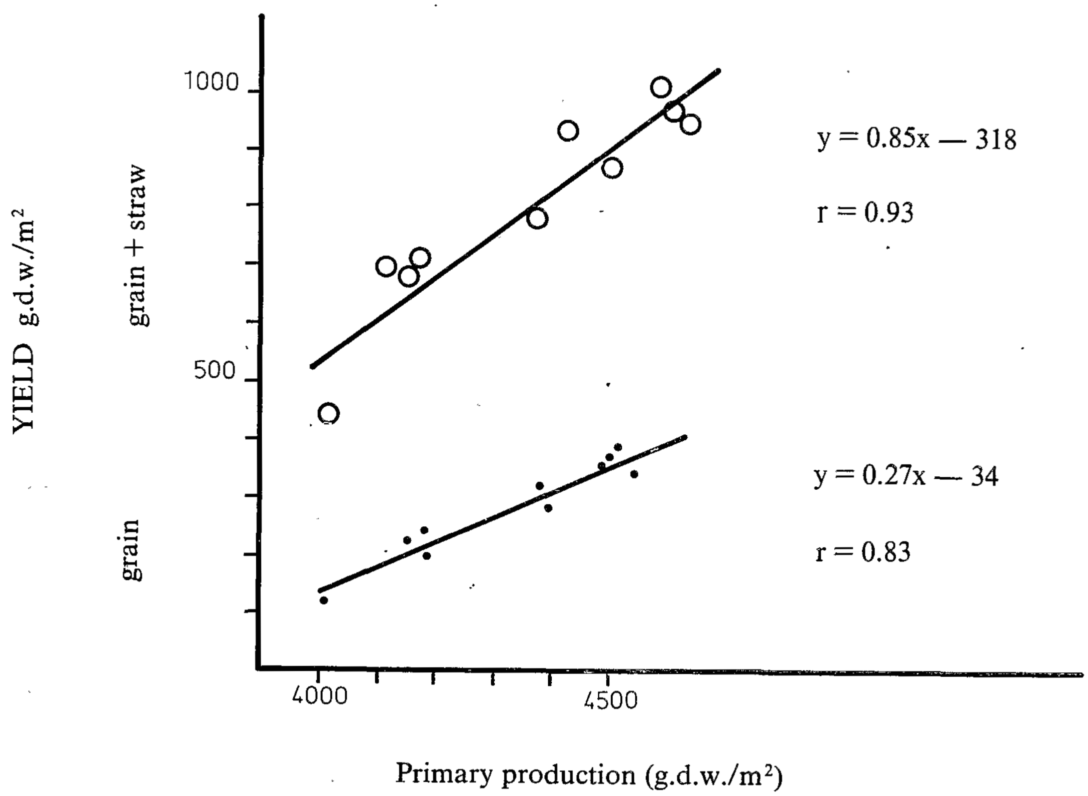


Figure 4. Relationship between yearly primary production and yield in rye agroecosystems (Kukielska unpublished).



If yield consists of several compartments of primary production then almost linear relationships can be expected between total net primary production and yield because of strong autocorrelation between theses two characteristics. In situations where yield consists of a small part of net primary production, low, if any, correlation could be expected because of compensation in growth rates of various components.

CONCLUSIONS

The driving force of any material transformations is energy. Thus, knowledge of energy flows, as well as rules of energetics, denote the change from inventory or static stage of scientific understanding to a dynamic one that permits management or engineering of the system under question.

Application of energetics to various fields of science not only deepened understanding of phenomena but also permitted explanations overcoming specific characteristics of these explored fields. Thus, real integration of physical, chemical, pedological, climatological, and biological processes could be obtained. Also influences exerted by man could be evaluated in terms of energy providing a suitable basis for economic evaluation. It should be pointed out that even such characteristics of environment as quality of air or water which are omitted in many traditional economic evaluations because of lack of quantitative values, could be easily included by evaluation of the energy cost of their regeneration or production.

An energy approach to agro-ecosystems is a basic requirement of modern science enhancing evaluation of total system functioning. To be explicit, energy flows can be arbitrarily divided into a) climatological (heat balance of environment) or b) biological that is flow of energy channeled by chlorophyll activity, and c) energy provided by men to the system in order to obtain specific agricultural goals.

In agroecosystems man shuffles these flows in order to achieve specific products.

It has been shown that the total primary production is less variable in various crops and years than harvested yield.

When comparisons are made of primary net productivity in cultivated fields, grasslands and forests of the temperate zone, the convergent values are found if a correction is made for the growth period. This finding is an expression of the known result of biochemical analysis showing that basic processes are almost identical in all photosynthetic organisms. Thus, the length of the growing season is a very important factor in primary production control in agroecosystems. The second in the rank among controlling factors is probably the water regime. Water is not only the ultimate source of electrons for reduction of CO_2 in photosynthesis but should be considered as a reactant of many biochemical processes. Water concentration in the cell influences enzyme action as well as performance of many physiological processes. Through control of the cell's turgor water influences plant structural characteristics too.

It seems that fertilizers have much stronger effect on yields than on total primary production. This is due to the fact that crops were selected to be responsive to fertilizer treatments by increase of yields. Thus, increase of yields due to progress in agriculture and the slight reaction of primary production to increase of fertilizer means that the input of plant debris into the soil is simultaneously declining. In other words, an intensification of agriculture undermines the regeneration processes of humus. To improve the regeneration of humus fore or after-crops are inserted in the rotation between the main crops. These are harvested for feed for cattle or are ploughed under as a "green manure". In the experiments carried on in the Department of Agrobiology and Forestry in Turew it was shown that fall seeded rye harvested in spring for forage provided additionally about 360 $g.d.w.m^{-2}$ (underground parts of this fore-crop) for humus regeneration.

Balance of organic matter providing regeneration of humus and plant nutrients is essential for long term management practices in agroecosystems. Fertilization, and many forms of tillage activity increase decomposition processes as well as crop export. Wind and water erosion decrease storage of humus in soil. Many of these effects are tied to microbe bioenergetics which is very flexible under field conditions. Thus, for example, turnover rates of microbes vary by factors of ten due to energy sources, physical and chemical conditions as well as biological interactions. Also resynthesis efficiency of dead cells by microbe populations varies by a factor of several units. These and other recently discovered functional characteristics of microbes have shown their high flexibility in decomposition processes.

Animals also play important roles as control mechanisms on the rate of decomposition, especially due to interactions with microbes. It was found in studies on total heterotroph respiration carried out in Turew, Poland, that the ratio of energy contained in primary production to energy utilized by the total set of heterotrophs is 2.1 : 1 in rye fields and 1.7 : 1 in a field with a forecrop of rye and potato as the main crop (Ryszkowski, 1975; Golebiowska and Ryszkowski, 1977). Such a high ratio is characteristic of early successional stages in natural ecosystems (Odum, 1971). In natural forest the ratio of energy contained in primary production to energy respired by the total set of system heterotrophs is 1.2 : 1 (Woodwell and Whittaker, 1968).

Thus, production of a unit of biomass in forest is correlated with much higher energy loss than in Turew cultivated fields. The relationship between input of organic matter and heterotroph respiration is poorly known. It seems that these two parameters are positively related while the form of the relationship is not linear. Thus, according to Golebiowska and Ryszkowski (1977), an input of 1882 kcal. m^{-2} per year contained in plant debris was related to 2498 kcal. m^{-2} per year respired by heterotrophs in rye field. While an input of 6088 kcal. m^{-2} per year resulted in 3957 kcal. m^{-2} year respired by heterotrophs in a field with rye as forecrop and potato as main crop. Thus, increasing organic matter input was positively correlated with an increase in respiration, but the ratios between these parameters were different in the two situations.

Complicated and very little known relationships between input of organic matter and heterotroph respiration, to say nothing about humification (generation process of humus), are the reasons why balance of organic matter in soil is achieved today by trial and error methods.

A decrease in soil organic matter was observed in many situations when natural ecosystems were converted into agroecosystems. For example, Martell and MacKenzie (1980) have shown that after 50 years of cultivation, organic matter declined 30 to 50 % on clay loam, sandy loam, and silty loam soils. Similar results were reported by Meints and Peterson (1977) who showed that during 30-37 years of cultivation organic carbon was reduced by 42-44 % and the effects of cultivation can be observed to a depth of 120 cm in many cases. The loss of organic matter is enhanced by soil erosion processes which diminished stocks of humus in Canada and USA (Ketcheson, 1980).

Table 12. Influence of agriculture on humus content in chernozem soils (Lavrentev 1972).

Location	Ecosystem	Period of utilization	Humus contents in 0-30 cm. upper soil layer (g/m^2)	Humus loss (g/m^2)
Kursk region	Meadow steppe	Native	20320	—
USSR	Unfertilized cultivated field	67	15390	4930
	Fall field	16	18850	1470
Kharkov region	Steppe	Control	21870	—
USSR	Cultivated field unfertilized	30	19280	2590
	Cultivated field mineral fertilization N - 135 kg/ha P - 195 kg/ha K - 60 kg/ha for 4-years rotation	30	20880	990
	Cultivated field + manure 3300 g/m^2 for 4 years rotation	30	21470	400

Proper agrotechnology could prevent rapid diminution of humus stocks (Table 12). For example, a decrease in soil organic matter was observed when chernozem soils were cultivated without addition of manure to keep the balance of organic matter in soil. When manure was added in amounts of 3300 $g.m^{-2}$ for the four year rotation, a slight decrease in humus content was detected only after 30 years of cultivation (Table 12). Both Martell and MacKenzie (1980) and Ketcheson (1980) show the importance of grasses for humus regeneration. The above changes in soil organic matter were caused by a net increase of organic matter decomposition over humus generation, as well as by wind and water erosion.

The contribution of these various processes to observed changes are unknown. Nevertheless, the loss of humus is observed in many agroecosystems, and simultaneously decreasing water storing capacity of cultivated fields, and fertility is recorded. These side effects of crop raising are provoking environmental problems like "soil sickness", eutrophication of inland waters and raise many health hazards. The humus is the key regulator of the ecosystem nutrient pool and water supplies as well as important factor in "self-purifying" abilities of ecosystems. Thus, maintaining regenerative efficiency of humus formation is of utmost importance for ecologically sound agriculture.

One of the important achievements of modern ecology is to prove that the agroecosystems having a high production output constitute systems with a low degree of coupling to local matter cycles. Therefore, agroecosystems provide a low carrying capacity in holding many introduced compounds. The consequence of this ecological regularity is that an increase in regenerating and self - purifying abilities of an agricultural region ought to be sought for in a proper structure of cultivated fields, meadows, shelterbelts, groves, water reservoirs and so on. The evaluation of energy flow and matter cycling in the agricultural landscape constitutes a natural base for elaboration of farming optimization principles taking into account economic effects and protection of the environment.

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