VINBERG G.G. 1948

The efficiency of plankton in the utilization of the sun radiation.

Briroda, 12, 29-35.

Translated by Mrs J. Talling.

Only from the axiom of an up-to-date natural science, develops a viewpoint, that the primary source of energy for all the living world comes from that part of the sun's radiation which is utilized in photosynthesis by green plants. With the numerous, well known and diverse peculiarities of structures of plants, the possibility is secured for sufficient absorption of the sun rays.

It is beyond doubt, as a result of the long history of processes in all types of natural communities, that there is established a specific level of utilization of the energy from the sun's radiation, reflecting its most fundamental nature.

Among these, even concerning the community of ground vegetation, in spite of the detailed studies on photosynthesis, how the physiological and biological processes are performed, and in particular their energetic aspects very little has been obtained of reliable quantitative information on the total degree of utilization of the sun's radiation by the vegetation under natural conditions.

Still less is known about the marine phytoplankton, and practically no quantitative, reliable data exist on the utilization of the sun energy by fresh-water plankton.

Thus the efficiency of utilization of the sun's radiation by natural communities has not been properly demonstrated with what so far has been obtained of reliable values, and it represents a great interest in many respects. This value could be used as rapid measure of the functional importance of a population (biom) of a specific portion of the biosphere.

In particular, it is very essential to know its value for the plankton, if only because water, as known, covers a big part of the earth.

A systematic study of the biotic balance of lakes was done by us in the course of a succession of summers, extensive material was obtained, which permitted us to compute a value for the utilization of the sunradiation by plankton in lakes, and to compare this with corresponding values for marine plankton and terrestrial vegetation.

It was started in 1932 [and done] with observations on the rate of consumption and evolution of oxygen by plankton in a series of lakes in the Moscow and Kalinin provinces (1,2). The observations were carried on with uncovered and covered bottles, which were placed for 24 hours at different depths, starting from the surface down to the bottom or to a zone where photosynthesis practically stopped. On the basis of these data it is possible to obtain a general quantity of oxygen produced in the presence of photosynthesis by phytoplankton in the whole water mass of the lake during an unit of time, for instance, for 24 hours, or for systematic observations during the growing season. Since between the quantity of oxygen given off and the quantity of bound energy, these is a strict and straight dependence, this same value being the well known quantity, which is being utilized in the photosynthetic energy [product].

As already mentioned, the data for the efficiency of utilization of radiant energy by natural vegetation with cover are surprisingly meagre. Furthermore, not universally adopted methods of calculation make the use of these data difficult. In these results, the values were often compared between themselves as well as with the expression in % of the sun radiation, but none the less, they had in fact entirely different contents. For instance, one author for the measurement of sun radiation used the maximal theoretical possible value at the latitude in question, - others used values differing greatly from these, based on actual observations on the radiation.

The efficiency of the utilization of radiation is often calculated for the growing season, the boundary of which to a great extent is an arbitrary measure, and different for different objects and conditions. In sorting out this present question from the confused literature, we have come to the conclusion that the best of all calculations were limited to two, appearing to be free from these shortcomings, namely: 1) The efficiency of the use of the total yearly radiation. 2) The maximal efficiency of the use of daily (24 hrs) radiation, which is reached at a certain point in the middle of the growing period, practically coinciding in time with the greatest rate of productivity.

The first value is for shortness called "U", the second "u" As a measure of the sun radiation, we consider the most accurately received radiation, not the maximal possible theoretically, but the observed quantity of the general sun radiation from the site, that is, the total direct and dispersed light.

The vertical columns 4 and 5 in the table show the primary production of plankton in 5 lakes obtained by thorough, systematic observations during the whole growing season, the above refers to the bottle method. The same quantity, expressed as % of the total sun's radiation for a corresponding time is shown in columns 6 and 7 of the same table. For the calculations of the annual general sun's radiation, we get according to Kalitin 7700 g. cal./cm^2/ year and the average of 24 hours in summary: June: 407, July: 398 and August: 285 g. cal./cm^2 (3).

The data in the table appear, up till now, to be the first reliable determinations of the efficiency of the utilization of sun radiation in fresh water plankton, unless a few should be considered, which are analysed below, whose authors have attempted to determine this value on basis of insufficient material.

About this first definition [determination], so different in different lakes, an index does not have a significance, for the measurements of radiation used were taken in Pavlovske and not at the site during observations on the lake. The total sum of the annual difference in radiation for different years is not big, and also the difference in the annual sum of radiation of the different periods at different low latitudes may not be big, and also the technical-physical-geographical conditions and height above sea-level. The practical authenticity of the used % calculations of yearly radiation, depends mostly on the manner of authenticity of determinations of the quantity of the primary products.

Many things could have accounted for variation in radiation at the moment of observation in the lake, for the specific value "u" and here a possible misestimation does not touch the order of the values and only important in the present original state of the study.

Table 1.

Names of lakes	Year of observ.	Primary product (kg cal./m²) Max. for 24hrs. in kg cal/m² date	kg/cal	Max. for a year (growing season in kg cal	The efficiency of the use of radiation. Max. for 24 hrs "u" (%)	Max. for year "U" (%)
Tjernoe in Kosino	1937	VI *	31.5	3014	7.7	0.40
Beloe I	1933	VIII *	16.6	1737	5.5	0.24
Shitovo in Zalucha	1937	7-10 VIII	6.3	911	2.2	0.12
Kolomno	1937	23-27 VIII	4.9	447	1.7	0.06
Beloe II	1937	3-6 VIII	1.5	155	0.4	0.02

Footnote: * average diurnal of the present month.

In the table, the sharp differences between the last values attract attention - of the very low efficiency of utilization of radiation in lakes. From Beloe II, with little productivity of plankton up to the high efficiency of polytrophic lakes. This is characteristic of their vigorously blooming waters with bluegreen algae.

Without being mentioned in the table, we did, with the same method, but singly, [make] observations, in July and August, on 31 lakes of the Moscow and Kalinin provinces. These data can also be considered, owing to the regular relationship [correlation] which exists between the maximal daily product and the product for the growing season, which practically equals the annual production. It has turned out that if the former value is expressed as a % of the second value, then for the 5 lakes (see table) we get the following range of figures: 1.04, 0.96, 1.00, 0.84, with an average of 0.92%. In all cases the maximal daily primary production is near to 1% of the annual. Making use of this empirically found regularity, multiplied by the maximal daily production, it is possible to get a certain introduction to and a value for the yearly production.

About the investigations in the area of primary production of plankton of the lakes in July and August, it is most often close to the average of the values, as shown in the table. Therefore for the lakes of the central region of the European portion of USSR, "u" is usually 2-5% and "U" close to 0.25%.

In the literature there are 4 well known attempts to determine a value "U" for freshwater plankton. Riley's (5), on basis of observations with the bottle method, on the evolution and consumption of oxygen in lake water. For lake Linsley (Conn. USA) he obtained 0.056 %. In reality, however, this value must be much higher for that lake, because Riley's observations began in the middle of September and were finished in June, and did not include the most productive period. Furthermore, the value for radiation which was used, 593.1 g cal./cm^2/day (216.5 thousand g cal./cm^2/year), appears to be the theoretically possible at the present latitude, but not a value that is based on actual observations, which should be about 2 times less (from Kalitin, N.Y. 95, Washington 122 thous. g. cal.). Manning (6) determined the average chlorophyll content of water in a series of lakes (Wisc.USA) and found that from 1.6 - 14% of incident light on the lakes is absorbed by the chloroplasts. On the basis of these measurements, the intensity of photosynthesis of culture of alges at different depths, with parallel measurements of radiation, Manning finds that the utilization is 2.7% of the energy absorbed by the chlorophyll. He computes, that in [the presence of] photosynthesis the plankton uses from 0.043 - 0.38% of the energy from the sun. As there was no possibility for us to make the acquaintance of the original of this work it is difficult for us to evaluate this value. In any case it is clear that they have a very common character, got by indirect means and with much help of assumptions.

In the specialized work on the energy-budget of lake Mendota, long-term observations on the quantity of plankton in this highly productive and well-studied (good study) lake were used by Juday (7), who obtained for "U" 0.27% (Wisc. USA). The yearly value of radiation received was 119000 g cal."cm^2 from observations from Madison. There was placed as a base for the calulations of the yearly product of the plankton, - and which was obtained by means of a symbol of multiplication for the average quantity of plankton (biomass), - a completely arbitrarily chosen coefficient of 26. The conditionality of the caluclations of the production with the help of an arbitrary coefficient emphasizes the ignorance, which Juday makes use of for the same purpose, but then with a coefficient of twice the size, 52 but in later paper (8) concerned with the same lake, he assumes a coefficient of 12. Lindeman (9) by analogous means calculated the value "U" for the lake Cedar-bog, for which he obtained 0.1%.

The very most this can lay claim to have shown is an attempt to obtain for the efficiency of utilization of the sun-energy this "form value", which the authors of these calculations themselves acknowledge. From his investigations solely is it possible to expose what he is talking about, when in our case it is usually about a few tenths of a %. In reality, the difference of the individual values are far from convincing, and to draw some conclusions from these comparisons, which Lindeman tried to do, was not justified.

On the eastern shore of USA, Riley (10) determined with the flask method, the primary product of marine plankton in the strait of Lond Island. All was done with 70 determinations, of unequal distribution in the course of the year. Observations were limited to depths of 1m., with 3-4 daily exposures of bottles. The rate of oxygen given off in photosynthesis fluctuated within very wide limits but on average turned out to be equal to 0.466 g/m^3 for 24 hrs. Riley obtains the primary production under a m^2 of surface by multiplication of this value by 10 and 15, as he supposes that within these limits the compensation point of photosynthesis is located. The author himself regards the "problematical" obtaining by such means of a value, the primary production under m^2. Assuming for the average diurnal radiation 300 g cal. $/cm^2$, Riley found an "U" equal to 0.58 - 0.82%.

The same author did analogous observations on 2 other regions by the west Atlantic Ocean. So, with the help of a series of arbitrary assumptions he, using his observations, arrived at the conclusion that the primary production of plankton in the region of latitudes 23^{o} - 38^{o}N equals 530 and for the region 38^{o}-41^{o} N 320 g. of carbon under m^2 in a year. Hence, to obtain calories and accepting the former daily energy as for the yearly radiation of 130 and for the latter 120 thous. cal./cm^2, than according to this we obtain for the value "U" 0.38 and 0.25%.

Using these data and comparing them with the results of attempts of several other authors to calculate the product of marine plankton on the basis of seasonal courses of biogenesis of the elements and other courses, Riley draws attention to the fact that the data have not shown an important difference dependent on latitude. It is well-known, in contrast to the above, that the biomass of plankton increases sharply at high latitude. Therefore, this opinion of Riley's is again insufficiently supported by factual material and obtains a especially great interest. [Footnote: reference to Riley's paper of 1944 in Am. Scientist 32: 189 " which we do not posess and which I did not see"]

On the basis of a not large number of short duration observations with the flask method, Shirshov (11), with a series of bold assumptions, determined the primary production in the east Siberian and Karskan seas as equal to 428 and 530 g glucose m^2/year. Hence, receiving a yearly radiation of 56000 g cal./cm^2 (observations in the bay of Tikho), we obtain for the value "U" accordingly 0.29 and 0.35%.

Perhaps this difference of the primary product of plankton even in adjoining parts of the sea is exhibited by the carefully carried out work in the Copenhagen Laboratory of Krogh, by the investigations of Nielsen (12), who with specific observations around the year (using the bottle method) as well as 24 hrs exposures of the bottles at 6 depths levels, empirically, without any additional assumptions, determined a value for the primary production of plankton in the N-W part of the strait of Helsingör, and which is expressed altogether as 130 g glucose per year and m^2. Hence, taking for that region correspondingly that the yearly sum of the general radiation is equal to 70000 g cal./cm^2, we obtain for "U" 0.6%.

Repeated attempts were made to determine a value for the primary product of the marine plankton with other methods, for instance, based on the seasonal course of events of biogenetic elements, but these could only give the minimal value of the product and were actually brought to a value, smaller than previously mentioned but on the same order.

[Footnote: From this original, interesting and principal respect, in examing the quantity of primary production of phytoplankton in the arctic sea by Yashnov (1940). The method of calculation is given in a previous paper by the same author (1939), the result being a return to the calculations of the product of phytoplankton, which were based on quantitative calculations of the main representative of the zooplankton, Calanus finmarchicus, the rate of its respiration, giving an idea about the requirements of nutrient. The results from Jashnov's calculations, I regret to say, could not be used owing to wrong assumptions. About those data from Marshall and Orr, Yashnov writes that 1000 mature individuals used in an hour in the summertime 0.33 cm^3 of oxygen " or 4.7 mg" and further: " in the winter 0.29 cm^3 or 4.1 mg. According to the fifth point, we got during the summer 0.19 cm^3 or 2.7 mg and during the winter 0.14 cm^3 or 2.0 mg. " Everywhere the intensiveness of consumption is expressed in milligrams with an error of 10 times. It is not difficult to be convinced, that there is a final value for the calculations and it ought to be appropriate with a figure to reflect on these results.]

According to the up-to-now, insufficient studies of this problem it is only possible to say that the primary production and the efficiency of the use of the sun-energy by marine plankton is expressed approximately by the same value as in freshwater lakes along with the productivity of plankton. This result is interesting and at a first glance unexpected. It is well known, that with the big transparency of marine water, photosynthesis in the sea spreads to considerable depths, more so than in freshwater. In freshwater the greater intensity of photosynthesis in the upper layers compensates for the fact that it is less widespread, as far as depth goes. Considerably more, and even so not enough is known about the efficiency of utilisation of the energy from the sun's radiation by the terrestrial vegetation.

In books of that general character, up to recent times, one often comes across the statement, that the ground vegetation utilizes 0.1% of the sun radiation, for which a reference is made to the work of Schroder of 1919 (14). In fact, the calculation of Schroder, out of necessity, had approximations and was insufficiently based, and this value expresses the utilization of the terrestrial vegetation only with a total sum of radiation, which fits according to the theoretical calculations of all surface terrestrial regions. It is characteristic, that because of insufficient data, Schroder completely neglected the photosynthesis of marine plankton.

It is known (15) that the yearly product of organic matter on one unit area, that different fields have, both cultivated kitchen garden and forest, is expressed close to a value of 7000 - 8000 kg/ha of organic matter. Let us assume for an approximate calculation, a yearly radiation of 100000 cal./cm^2 the calorie content of the organic matter as 4500 and the expenditure for respiration as 20%, then we obtain for the value "U" 0.38 - 0.43%.

The results of the first out of these former attempts to calculate the efficiency of the utilization of the sun's radiation by measuring vegetation belongs to Putter (16), thus receiving a wide publicity and they were incorporated into summaries of photosynthesis. Putter used statistical data of unusually high harvests, for instance, for wheat he judged the harvest data of the grain to be 4700 kg/ha. The energy content of the vegetable mass he obtained from analytical chemical data, the expenditure for respiration he put equal to 15%. For cereals, potatoes and beets, the efficiency of the utilization of energy during the vegetative period came to 2.5 - 3.5%. But Putter used old data, obtained in an indirect way, for the quantity of the sun radiation, which he assumed equal to 5000 g cal./m^2/ year, which at least is two times less than the true value. Accepting from Putter's calculations the calorie content and taking the value for the sun's radiation as 70000 g cal./cm^2/year, which also is below the value observed in Middle Europe, we obtain "U" equal to 0.59 - 1.07%.

In more recent times, Transeau (17) in a special paper, computes the utilization of radiant energy by wheat from results of average statistical data on yield of wheat (Wisc. USA) and initiated a series of corrections for the expenditure of respiration and so on. The utilisation of energy for the growing season he determined as 1.6%. As the annual radiation in that area (Wisc.) equals 119000 g cal./cm^2 and with the material from Transeau's paper we obtain for "U" 0.68%.

The most complete and authentic information on the utilization of sun radiation, free from arbitrary assumptions, based on careful results of investigations over a period of 4 years, is that of Doyarenko (18), who determined directly the caloric "capacity" of very high yields of 10 different cultivations in experimental plots of land near Moscow. The data are expressed as % of radiation for the growing season (2.05 - 5.10%). According to the data and the sum of the annual radiation for year 1919, 77000 g. cal./cm^2, we obtain for the value "U" from 0.45% (vetch) up to 1.19% (wheat) with the arithmetic mean of 1.1% (without correction for the expenditure of respiration).

Boysen-Jensen (19) derived from special data of measurements of the yearly product of the beech forest, a value, accounting for the expenditure of respiration. According to his determinations, the yearly product of the beech forest works out to be 10.48 T/ha. of dry matter (weight), which approximately corresponds to 4700 Kcal/m^2. Hence for the quantity "U", we obtain 0.68% (with an annual radiation of 70000).

The same author obtained, for the yearly product of a mustard field allowing for expenditure for respiration, a value of 12.7 T/ha dry matter, which approximately would correspond to 0.83%.

The productivity of littoral weeds of marine algae, according to detailed quantitative studies by Morozova-Vodyanitskaya (20) conducted in the Novorusski-bay, was very close to the productivity of the ground vegetation. The greatest productivity of a region was 17537 g fresh matter/year, which in order to incorporate it into the present work, would correspond to 2883 g dry matter, with 20% allowed for ash content and a caloric content without ash material equal to 4300, this comes out to be 0.88% of the total radiant energy for a year (113000 g cal/cm^2 - Feodozia, 1930). Discounting the expenditure for respiration we obtained for "U" approximately 1.05%. In average, for the whole area investigated for productivity of a field, the corresponding "U" was 2 times less than this maximal value.

The work of Kireeva and Shchapova (21) dealing with determinations of a littoral biomass of weeds from the Mangislak region of the Caspian sea, brought out a significantly smaller quantity of biomass. According to the present authors, we obtained, that the weeds Ruppia and Zostera on a sandy-musselshell soil in an average had a biomass of total 500g/m^2 of fresh matter. Not great under these circumstances, a maximal biomass of 1718 g/m^2, corresponding to a value of "U" at 0.1%. The above authors quote a very high maximal biomass, in a spotted distribution of the weed Chara intermedia, 29,840 g/m^2 living matter. For the calculations of "U", it would be necessary to know the ash content, probably very high in this species, With an ash content of 40-50%, "U" would be in the order of 1%.

Sufficient data have been brought out to show, that the utilization of the solar energy of ground vegetation with cover of various types of its own kind and of [weed of] water plants in the temperate zone, expresses itself very close to a value, usually not far from 0.5 - 0.8%, but will reach 1.2% and higher. Consequently according to our data, in their relation to the capacity of utilization of the sun radiation, freshwater plankton attain this only in [the circumstances of] high productivity lakes and the values are significantly lower than for the terrestrial vegetation or submerged weeds.

There is very little data available, suitable for evaluation and from which is would be possible to consider the value of the maximal utilization of daily radiation ("u").

According to the measurements of Doyarenko in the most productive month (June), the efficiency of the utilization of sun energy by wheat amounts to 8.78% and for rye 7.59%. Assuming 25% expenditure for respiration, we obtain for "u" 11.0% and 9.5% resp.. By exbluding the high utilization of the daily sums of radiation, it follows from data of Boysen-Jensen on the increase of dry matter in a mustard field, which in a period of 23-30th of June was equal to 0.17 T/ha, which corresponds approximately to 18% of the daily average radiation in June in Pavlovsko.

To judge from what here has been reported, it follows that there still exist insufficient data on the utilization of the sun radiation of ground vegetation with cover at the middle latitudes, submerged weeds, marine and freshwater plankton, to be expressed with a close value (the 10th.%

of the yearly sum of the total sun radiation)- it being, that the value for the efficiency of utilization of the radiation by freshwater plankton, apparently, is rather less suitable than for other types of natural vegetation.

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x [In original a misprint - 1944 is quoted - 1914 is correct.]

Notice

Please note that these translations were produced to assist the scientific staff of the FBA (Freshwater Biological Association) in their research. These translations were done by scientific staff with relevant language skills and not by professional translators.