On the Dynamical Relationship between the Production of Phytoplankton
Community and the Morphometry of Lake, and its Meanings
for the Ecological Succession

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CONTENTS

Introduction

For the clarification of the progressive changes of the phyto-
plankton community in the earlier stage of hydrarch succession,
the analysis of microfossile algal flora or chemical constituents
of lake sediments have been carried out by several investigators
(Lundquist, 1927; Hutchinson & wolack, 1940; Lindeman, 1942;
Fjerdingstad,1954). These studies could give much descriptive
informations on the sequences of hydrarch succession and on the
relationships between these changes and the environmental condi-
tions, but provided us little explanation on the mechanism
through which the progressive change of the phytoplankton commu-
nity took place under the effect of climatic, edaphic and topogra-
phic conditions.

In general, the following two changes may be expected as the
important causes of the lake succession from oligotrophy to eutro-
phy : 1) gradual shoaling of lake basin by the progresseive accu-
mulation of sediments, 2) gradual eutrophication of lake water
caused by accumulation of nutrient salts. For inducement of
these two gradual changes, inflow of allochtonous organic matter,
sand, or mud is often significant(cf. Livingston et al., 1958).
However, autochtonous substances originated in the production
of lake plant community seems to be generally playing an important
role. It has been well known that living green plants, the
primary producer in lake, generally accumulate the nutrient salts
in their cells in higher concentration than in the external
medium (cf. Hoagland & Davis, 1923; Matsue, 1952). Then,
sedimentation of dead plankton organisms to lake bottom, even
if partly mineralized by bacteria in the course of their settling,
must results/ in the gradual shoaling of the lake basin and the
gradual accumulation of nutrient salts in lake water by coupling

with the alternation of stagnation and circulation of lake water.

The lake depth and the concentration of nutrient salts in lake water usually have large limiting effects on the production of phytoplankton community. Then, the changes in the environmental conditions such as eutropication of lake water and shoaling of lake basin must bring about the change in the productivity of phytoplankton community, which contrariwise gives the change on the rate of shoaling and eutrophication.

Thus, we can expect the dynamical mutual action between the production of phytoplankton community and the lake environments. The dynamical processes of such a mutual action will bring about the progresseive and irreversible changes of plant community in lake and its environment in lake over a long period of years. Therefore, it is not too much to say that the analysis of successional process in lake becomes possible only based on the primary production in it.

Monsi and Oshima (1955) clearly disclosed the general law of the successional process of land plant community through the theoretical consideration on the mutual action between the community and its environment from the view point of dry matter production. Concerning the phytoplankton community in lake, Hogetsu and Ichimura (1953) have already pointed out an important role of the production in the process of succession. Beside their work, few analytical investigations have been done up to the present from this point of view.

The purpose of the present study is to analyze the process of ecological succession in lake, especially the process from oligotrophic to eutrophic state, on the basis of the production of phtoplankton community. For attainment of this purpose, it is necessary to successively clear up the following problems :

First, in what ways and in what degree the production of phyto-
plankton community is affected by either nutrient salts content
in lake waters or morphometry of lake, especially the mean depth
of lake, which changes gradually in the course of succession.
Second, how progressive changes such as the accumulation of nutri-
ent salts and the shoaling of lake basin are controlled by the
production of phytoplankton . Third, how the dynamic mutual re-
lations between the production of phytoplankton community and the
environmental conditions in lake are influenced by climatic and
edaphic conditions. Finally, to derive the general law of the
process of hydrarch succession from theoretical consideration on
the results in these analytical investigations.

In the present paper as a first step to the study in this
direction, the author attempts to analyze the first problem and
then a theoretical consideration on the second problem, making
clear the significance of the dynamic mutual action on the process
of hydrarch succession.

II. General Procedures

The methods of chemical analysis of the lake water and the
culture of algae employed in the present study are as follows.

a) Analytical methods

Nutrient salts. As a preceding treatment for chmical analysis,
200 ml. of the smpled lake water were concentrated in an evapo-
rating-dish to about 50 ml.. Total nitrogen: Total nitrogen
was determined by the usual semi-micro Kjeldahl method. Total
phosphorus: After the concentrated sample was digested with a
small quantity of sufuric acid, nitric acid and hydrogen peroxide,
and neutralized with liquid ammonia, the concentration of inorga-
nized phosphorus was determined colorimetrically by Denigie-Atkins

method. Total iron : The iron concentration of the neutralized solution described above was determined colorimetrically by addition of acetate buffer solution containing α-α'-dipyridyle and hydroxylamine.

Chlorophyll content. The amount of phytoplankton was routinely estimated from the chlorophyll content of the sampled water. The method for determination of chlorophyll content employed here was essentially similar to that described by Hogetsu et al. (1952) and Ichimura (1956).

Photosynthesis. The measurement of the photosynthetic activity of the algal population sampled in the field was usually carried out in the laboratory. The sampled lake water, brought in the laboratory as soon as possible after sampling, was filled in transparent and blackcloth-covered bottles of about 100 ml., then these bottles were placed horizontally in a running tap water bath at a constant temperature (about 20-25°C) under artificial illumination. Different light intensities were obtained by varying the distances of the bottles from the reflectorlamp (300 or 500 watt). After the 2-3 hr. illumination , the increse or the decrease of dissolved oxygen in the bottles was determined by Winkler's method, and then the values of transparent and blackcloth-covered bottles were summed up to obtain the photosynthetic rate. In the case of the cultured algal population, the procedure used was essentially similar to that described above.

b) Culture methods

To obtain a clue of the analysis of the given problems or to ascertain the results obtained in natural waters without any definete experiment, culture experiments were frequently performed under various conditions. Chlorella sp., which was purified by

the author in the laboratory, was used as an experimental material on account of the facility of culture. The material used for the measurement of photosynthetic rate was usually cultured in the conical flask of 500 ml. capacity containing modified Detmer solution, diluted to 1/5-1/10 concentration, in which the equivalent KNO_3 in nitrogen was substituted for $Ca(NO_3)_2$. The algal suspension was usually illuminated by a fluorescent lamp and stirred up with a constant bubbling of air to prevent the sedimentation of algal cells. For the purpose other than that described above, algae was cultured in the medical glass cups of 350 ml. capacity. Each cup contained 300 ml. of the culture medium of the following basic composition : 20 ppm. of KNO_3, 10 ppm. of $MgSO_4 \cdot 7H_2O$, 10 ppm. of $CaCl_2$, 1 ppm. of KH_2PO_4, 0.5 ppm. of ferrous citrate and trace of microelements. The cultures were performed at ordinary room temperature under the constant illumination of four 40-watt daylight type fluorescent lamps (about 4000 lux at the surface of the culture pots) and usually duplicated. Every other day throughout the experimental period, a few drops of $NaHCO_3$-saturated solution were added to the culture medium to prevent the deficiency of the carbon dioxide source.

The yield of algae was measured by determining the extinction value of algal suspension with the following formula

$$E = \log I_0/I$$

where E is the extinction coefficient of algal suspension of 1 cm. thickness in red light (640 mu) and represents the relative concentration of algal suspension, I_0 and I are the readings of galvanometer in the fresh medium and in the sampled algal suspension respectively. Extinction coefficient, however, as pointed out by Rhode (1948), is not a direct measure of the amount of algal substance, but to a large extent varies by other characteristics of cells, especially by chlorophyll content, which are dependent on the culture conditions. As chlorophyll is the most important

substance in the photosynthetic process, this value may be considered to express approximately the amount of the production unit.

III. The dependency of the Production of Phytoplankton on the Mean Depth of Lake.

It has been long recognized that a shallow lake is generally fertile and supports the life of many organisms, while a deep lake is barren and produces only a few organisms. By examinating the descrptive data obtained in many German lakes, Thienemann (1921) had found a close relationship among the shape of lake basin, nutrient salts concentration and the quantities and qualities of the lake organisms, and then presented the notable concept of lake-type. In this case, the morphometrical character of lake basin, especially its mean depth, was consideded to be the most significant factor in determining the lake-type. After that, many investigators (Rawson, 1952,1953,1955 ; Hogetsu et al., 1952) have demonstrated that this conclusion was subtantially correct in the lakes of temperate region. However, it had no applicability for the tropical lakes (Ruttner, 1931). Recently, Frey and Stahl (1958) reported that the controlling effect of morphometry of lakes on the production may be significant in the arctic lakes as well as in the temperate ones.

Regarding these close relationships between the lake depth and the production, various explanations have been presented to date (Thienemann, 1928; Rawson, 1935; Hogetsu & Ichimura, 1953 etc.). As these explanations, however, have been done only qualitatively and arbitrarily, there remains many problems to be analyzed. In the present chapter the author dealt with the detailed analytical investigations on the actual relation

between the depth and the production of phytoplankton community in Japanese lakes.

In connection with the climatic factor, the depth of lake generally governs the underwater illumination, temperature, and the circulation lake water. Moreover, in connection with the edaphic factor of drainage area it will determine the initial concentration of nutrient salts in lake water as pointed out by Rawson (1935,1953). In this case, the utilization degree of the nutrient salts by phytoplankton is controlled by their vertical circulation of lake water. To analyze the controlling effect of the morphometry of lake on the primary production, therefore, it will be necessary to analyze the relationship between the lake depth and the light intensity, temperature and nutrient salts concentration in the lake water.

It is noteworthy here that the circulation of lake water gives also a large effect upon the vertical structure of phytoplankton community (productive structure) as well as the effect upon the circulation of nutrient salts. In consequence, the significance of the mean lake depth for the production of phytoplankton community differes greatly either during cir-culation period or stagnation period.

I. Production of Phytoplankton Community during Circulation Period.
(a). Relation between the amount of phytoplankton and mean depth.

In deeper lake, the complete circulation of lake water is usually limited only in spring and autumn when temperature at any layer becomes uniform. The annual maximum yield of phytoplankton community is observed only in these seasons. In shallower lake, however, higher rate of production is maintained throughout the year. It is interesting to compare the amounts of phytoplankton in both

types of lakes in the circulation period. The mean chlorophyll
content measured in the euphotic zone of Japanese lakes with
various depths during a circulation period (Ichimura, 1956;
Ichimura & Saijo, unpublished), is plotted against the mean depth
of the corresponding lake in Fig. 1 on the ordinate scale and in
Fig. 2 on the logarithmic scale. These figures show that there
is a remarkable inverse relation between the lake depth and the
chlorophyll content in unit volume of the water, namely the density
of phytoplankton population, although this relation becomes
contrary in a too shallow lake. Assuming that phytoplankton
distributes homogenously in a water column for this period,
which appears to be similar to the actual state, the product of
the chlorophyll content per unit water volume by the mean depth
will approximately give the total amount of chlorophyll per unit
area of water surface. In Fig. 3 the relation between this product
and the mean depth is illustrated. Apparently, this relation is
similar to that shown in Fig.2.

Here one must pay attension to the fact that the decrease of
chlorophyll content in a too shallow lake was in parallel with
the luxuriant growth of rooted aquatic plants (cf. Lake Tega).
In the lakes of similar depth with the poor growth of rooted plants,
a dense bloom of phytoplankton could be usually observed (cf.
Jōnuma). Such antagonistic correlation between phytoplankton
and rooted aquatic plants, must be of a great ecological signi-
ficance on the process of hydrarch succession.

As described before, the lake depth gives an indirect effect
on the production of phytoplankton community through the change
in the environmental factors. Hogetsu pointed out the importance
of the decrease in underwater light intensity with depth for this

phenomenon and demonstrated it by the culture experiment of
Chlorella in different thickness of culture medium. In the cul-
ture with Detmer's solution (diluted to 1/10) under the condition
of constant stirring and artificial illumination (about 4000 Lux),
the yield of algae per unit volume of culture medium was always
inversely proportional to the thickness of the medium (Fig.4).*
This is apparently due to the decrease in photosynthetic rate
of algal population caused by the decreasing average light inten-
sity in algal suspension with depth. The similar situation may
also be expected to some extent in natural waters.

It has been frequently recognized, that the growth of phyto-
plankton in natural waters was strongly limited by the amount of
nutrient salts, which correlated closely with the character of
lake basin (Juday & Birge, 1931; Naumann, 1932; Yoshimura, 1936
etc.). Consequently, it is very doubtful whether the morphometric
control of the production of phytoplankton community is always
caused by the similar situation to the results of the culture ex-
periment obtained under the optimum nutrient condition. The
author surmises that , in many cases, the production might be
controlled more effectvely by the differences in the amount of
available nutrient salts rather than that in the average light
intensity in the water column.

b). Difference in the nutrient salts content in the lakes of
    various types and its significance for the growth of
    phytoplankton.

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* This experimental result was kindly made possible at the author's
  disposal by Prof. K. Hogetsu, to whom due gratitude is extended.

Previous works concerned with the relation between the growth of phytoplankton in natural waters and the nutrient factor have been mainly carried out on the basis of comparison of the amount of phytoplankton with the concentrations of soluble inorganic nutrient salts. However, the nutrient salts in inorganic forms found in the lake water are usually only one part of total available nutrient salts for the production of plankton substances, for the most part of them has been already absor-bed by phytoplankton. Especially, during a growing season of phytoplankton such as a circulation period the inorganic nutrient salts are exhausted (cf. Yoshimura; 1936, Sugawara, 19   , Hogetsu et al. 1952).

It has been often recognized that the nutrient salts bound in organic substances were actively utilized by phytoplankton (Chu, 1943; Rodhe, 1948; Ⅱ Ludbig, 1952; Harvey, 1953; Hattori, 1957; Abbot, 1957).   Therefore, it will be rather proper to measure the total content of nutrient salts than those in inorganic forms in order to estimate the amount of available nutrient salts for the growth of phytoplankton.

From this point of view, the author performed the chemical analyses of the total content of nitrogen, phosphorys and iron, which have been recognized as the limiting elements for the growth of phytoplankton (cf. Welch, 19   ).   From April to May and from November to December, as the nutrient salts and phytoplankton appears to be uniformly distributed in the whole water column, measurements were carried out as the only the surface water of various lakes.

The results obtained are given in Table 1.   The data indicate

that in the lake water of harmonic type the total nitrogen
content falls within the range from 0.15 to 1.20 ppm. . In general,
the contents of these nutrient salts are larger in shallower lakes
than in deeper ones. These relationships are also shown graphically
in Fig.5. Apparently, the curveliner inverse relationships
are found between the mean depth and the total content of each
nutrient salt as well as in the case of chlorophyll content (Fig.1).
Therefore, it seems likely that the controlling effect of the lake
depth on the production of phytoplankton community may be con-
siderablly responsible for the differences in the amount of
limiting nutrient salts.

On the quantitative relationship between the growth of phyto-
plankton and the concentration of nutrient salts, many investiga-
tions have been performed by the culture experiment using various
purified algae (Chu,1942; 1943;;Rodhe, 1948; Osterlind, 1949;
Gerloof & Skoog, 1954,1957). The minimum requirement of different
phytoplankters for various nutrient elements which were revealed
by their investigations are summarized in Table 2.

Comparing these values with the contents of the corresponding
elements in lake waters (Table 14/1 1 and 3), it is clear that
the content of nitrogen and phosphorýs in lake waters is much
lower than the minimum requirement of phytoplankton for the
optimum growth. On the contrary, the content of iron in lake
waters is rather higher than the minimum requirement, although
the relation of its content to the mean depth is very similar to
those in the case of nitrogen or phosphorus. It has been recog-
nized that iron content in lake water usually did not limit the
growth of phytoplankton (Yoshimura, 1936; Rodhe, 1948. Gerloff
& Skoog, 1957). From the relation above-mentioned, there will

be no reason to believe that iron is a limiting element for growth of phytoplankton in the lake concerned in the present paper, too. Concerning other major nutrient salts, chemical analysis has not been performed in the present study, but one can obtain the informations on the contents of them in some Japnese lakes from the Yoshimura's report (1936).

The data in this r/eport indicate that in the lakes of harmonic type the content of calcium is 3-20 ppm., magnesium 1-5ppm., and silicate 10-50ppm.. Considering these and the minimum requirement in Table 2, it is obvious that calcium and magnesoum are contained in the lake water far in excess of the minkmum requirement, but the content of soluble silicate is somewhat lower than the minimum requirement of some species of diatoms. In this case, however, it must be kept in mind that the profuse silicate is contained in natural waters not only in soluble but also in colloidal state. From the facts mentioned above, it may be possible to say that among various nutrient salts dissolved in the lake waters, nitrogen and phosphorus are the elemtnes present relatively in the least amount to the requirement for the normal growth of phytoplankton.

c). Changes in the yield of algae with varying the concent-
ration of nitrogen and phosphorus in the culture medium.

In order to clarify to what degree the nitrogen or phosphozus concentration in the lake water is limiting the production of phytoplankton, the culture experiment of <u>Chlorella</u> was primarily carried out in the medium of varying concentration of nitrogen or phosphorus was varied by adding different amount of $NaNO_3$ or NaH_2PO_4. In the culture for 53 days (20-23 C) the dependency of the final yield to the concentration of nitrogen and phosphorus

in the culture medium is shown in Figs. 6 and 7. Under the constant nitrogen or phosphorus supply and varying concentration of the other element, the yield of algal population augmented up to the maximum with the increase in phosphorus (Fig.6) or nitrogen concentration (Fig.7). After attaining to the maximum yield in the optimum concentration, there was no change or a slight decrease in yield with further increase in the nutrient concentration. Considering the fact that the upper limit of nitrogen and phosphorus concentration found in natural waters was 1.2 ppm. and 0.07 ppm., respectively (Fig.5), these figures may indicate that both nitrogen and phosphorus in natural waters are strongly limiting the growth of plankton algae.

As clearly seen in Fig. 7, in the culture of low phosphorus level as in the most primitive oligotrophic lake (0.005 ppm.) even sufficient supply of nitrogen gave only the least promoting or deteriorative effect on the algal yield. When the phosphorus level of culture medium increased, however, more marked increase in the yield was observed with increasing nitrogen supply. The increase in phosphorus supply into the culture of constant nitrogen level was associated with a marked increase in the yield even in the lowest nitrogen level which is lower than the lower limit in natural waters during a circulation period(0.15 ppm.). These results may suggest that the phosphorus content in oligotrophic lakes is limiting the growth of algae in a higher degree than nitrogen.

For clarifying the dependency of the growth of plankton algae on the nutrient level in natural waters, the ratio of nitrogen and phosphorus concentration in the waters was calculated (Table 1). The values obtained were plotted against the phosphorus level of

the corresponding waters in Fig. 8. It is clear that N : P
ratio in Japanese lakes during a circulation period lies within
the range from 30:1 to 10:1, and appears to decrease inversely
with increasing phosphorus level except in very shallow lakes.

The waters taken from the shallow eutrophic lakes in which
the bloom of <u>Microcystis</u> is found in midsummer or the rooted
aquatic plants are luxuriantly growing, have higher value of N:P
ratios namely higher nitrogen content than that expected from the
general tendency (cf. Fig.8). These situations, together with
the fact that river water has the most oligotrophic characters
as clearly seen in Table 1 (N:P ratio is 30:1 and phosphorus
level is 0.01 ppm.), may give many suggestions on the conside-
ration of the succession in lake.

The broken lines in Figs. 6 and 7 express the upper and the
lower limit of N:P ratio in natural waters. By examining the
increase rate of yield with increase in nutrient level near the
intersecting points of the broken and the solid lines, it will
become possible to clarify the limiting state of nitrogen and
phosphorus for the growth of plankton algae.

In the waters having the N:P ratio of about 30:1, the increas-
ing rate of the yield with increase in phosphorus level is very
large within the range of phosphorus level found in natural waters,
as evident in Fig.6. The increase in nitrogen level, however,
gives only the least promoting effect on the yield (Fig.7).
Namely, in this case, phosphorus seems to be predominantingly
limiting the growth of algae.

On the other hand, in the case of waters having the N:P
ratio of about 10:1, the increase in nitrogen level gives not
only the least promoting effect on the algal yield in the culture
of lower phosphorus level, but also a large effect in the culture
of higher phosphorus level (Fig.7). The increase of yield is
also induced by the external supply of phosphorus, but it becomes

gradually less marked with increasing the level of nitrogen (Fig. 6).

Considering these situations in comparison with the fact that t e total nitrogen content in the natural waters deviates in the range from 0.15 to 1.20 ppm., and the total phosphorus cntent from 0.008 to 0.07 ppm.(Fig. 5), it can be said as follows; In the X oligotrophic lake, the growth of phytoplankton is frequently limited predominantly by less phosphorus supply, and its controlling effect on the algal yield becomes gradually less with the increase of phosphorus level of lake waters. In eutrophic lake, however, the limiting effects of nitrogen and phosphorus appear in nearly the same degree.

The above mentioned relationship between the growth of plankton algae and the nutrient level was derived on the basis of the results from the culture experiment of Chlorella under varying nitrate and phosphate concentration. It must be noticed here, however, that the relation of the optimum growth to the nutrient level differs so much from species to species (Chu, 1942,1943; Rhodhe, 1948). Moreover, as evident from Rodhe's report (1948), the very large discrepancy is often found between the relation of optimum growth to nutrient level in the natural waters and that obtained in the artificial media, presumably due to existence of X unknown substances in the natural waters. Consequently, it may be inadequate to derive the ∅ conclusion on the dependency of the nutrient level in natural waters on the growth of plankton algae only from the results of present experiment. Then, it was designated to examine the relation between the yield of natural population and the nitrogen or phosphorus level in natural waters.

d). Relationship between the growth of phytoplankton and the
    nutrient level in natural waters.

For clarifying the causal relation between the yield of
natural phytoplankton population and the nutrient level, the
observations must be carried out in the water in which only
the nutrient salts is limiting the growth. In Japanese lake waters
the available nutrient salts are usually almost exhausted by the
luxuriant growth of phytoplankton throughout the period from
late spring to late summer. At that time, the phytoplankton
community in the surface water under sufficient solar radiation
and moderate temperature seems to be attained to its maximum
yield under given nutrient condtion. Namely, the growth rate
of the community is equlibrated with the death rate of it.
Then , present observation was carried out only as to the surface
waters of various lakes and ponds.

Species composition of the phytoplankton communities concerned
here was as follows; In the X oligotrophic or mesotrophic lakes
a dominant was <u>Asterionella</u> <u>formosa</u> in many cases(cf. Figs.
9 and 10). On the other hand, in the eutrophic lakes and ponds
a wide variation in the dominant species was observed in various
waters and times. The main dominants were <u>Synedra</u> sp., <u>Merosira</u>
sp., <u>Scenedesmus</u> sp., <u>Ankistrodesmus</u> <u>falctus</u>, <u>Chlamydomonas</u> sp.,
and <u>Microcystis</u> <u>aureus</u> etc. In spite of such a wide variation
in dominant species, the amount of phytoplankton was always esti-
mated from chlorophyll content in the lake waters not merely for
the facilitation of measurement, but also for the generaliza-
tion of the consideration. The nutrient level was estimated by
the measurement of the content of total phosphorus and
nitrogen in the sampled waters.

Figs. 9 and 10 show that there is approximately a linear relationship between the chlorophyll content and the nitrogen or phosphorus level which is plotted on logarithmic scales. It must be noted here that the deviating points below the straight line in Fig.9 have larger value of the N:P ratio than ones situated near or on the line. Comparing theis situation with the fact that the corresponding points in Fig.10 are found near or on the line, it will be clear that less supply of phosphorus, consequently the larger N:P ratio is responsible for lower yield of phytoplankton than that expected from the nitrogen level. Namely, the deviation of the results in Fig. 9 resulted from limited growth or increasing death rate due to less phosphorus supply. Just the contrary situation to this can be seen in the deviation of the values having small N:P ratio in Fig. 10.

In this case, naturally, the deviation caused by the difference in the specific characters of the dominant species must be considered. The results obtained in the waters with the same dominant species, however, are quite similar to the above described situation except for the following case.

As shown by the dark circles in Fig.10, the waters with the waterbloom of _Microcystis_ _aureus_ have an exceptionally higher chlorophyll content than that which could be expected from the phosphorus level. The dominant of blue-green algae has generally been recognized as growing in the waters having a higher nitrogen content.. Recently, Gerloff et al. (1954, 1957) have disclosed that the nitrogen requirement of _Microsystis_ _aureus_ is about sixty times as high as the phosphorus requirement. In consequence, _Microcystis_ will give a higher amount of chlorophyll in the waters of high N:P ratio than that which is expected in other

species from the phosphorus level. However, as the water-bloom of _Microcystis_ appears mainly in summer, this exception need not be considered during the circulation period.

Thus, it may become possible to expect the following relations among the yield of phytoplankton community , the nitrogen or phosphorus level and the ratio between them : In the waters having the N:P ratio of 9-10 to 15-17, the nitrogen and phosphorus content are nearly balanced with the ratio required for phyto-plankton (cf. Birge & Juday, (1922), and the yield varies with the nutrient level according to the linear relationship shown in Figs.8 and 9. In the waters of larger N:P ratio than 15-17, however, the amount of phosphorus becomes predominantly a limiting factor and the yield varies according to a linear relationship given in Fig.8. In the waters having the ratio below 9, nitrogen becomes a critical factor and the yield varies along a straight line as shown in Fig.9.

In natural waters the upper limit of nitrogen and phosphorus levels during the circulation period are 1.2 and 0.07 ppm., respectively, and the N:P ratio generally decreases with the increase of phosphorus level. The same conclusion on the relation-ships between the yield of phytoplankton and the nutrient level in the natural waters as the results of the culture experiment can be presented here. Namely, in Japanese lake nitrogen and phosphorus are highly limiting the growth of phytoplankton commu-nity. In the oligotrophic lake, the yield of community is conspicuously limited by the phosphorus supply. With the increase in nutrient level of the water, the limiting effect of phosphorus on algal yield is nearly balanced with that of nitrogen. Contrar-wise, the prominent limitation of the yield through less nitrogen supply can been hardly seen except for the case of _Microcystis_.

e). The theoretical explanation of the dependency of the production

of phytoplankton community on the lake depth.

As previously described, the denpendency of the production of phyto-
plankton community on the depth of lake may be partly responsibéle for
the restriction of photosynthesis of phytoplankton community due to the
decrease in the average underwater light intensity with the increase of
depth. In the present section, this effect will be examined quantitatively.

If the distribution of plankton is homogeneous, in all depth, the
relative light intensity at each layer in a water column can be expressed
by thefollowing formula as a function of the incident light (I_o) and the
extinction coefficient (α) of the lake water :

$$I_D = I_o \; e^{-\alpha D} \; \text{-------------} \qquad (1)$$

where I_D is the light intensity at the depth of D. The extinction coe-
fficient is markedly influenced by the amount of suspended matter in the
lake water. Kikuchi (1935), Ichimura (1956) and others have recognized
the fllowing re-lationships between the transparency (T) and the extinc-
tion coefficient (α) in many Japanese lakes :

$$\alpha = 1.9 \; / \; T \; \text{---------------} \qquad (2)$$

If the formula (2) is adopted here, the quantitative relationships be-
tween the extinction coefficient and the chlorophyll content of lake
water can be obtained from the data reported by Ichimura (1956), Saijo
(1957) and Ichimura and Saijo (unpublished). It appears clearly in Fig.
11 that there is a direct proportionality between the mean chlorophyll
contents in the euphotic zone and the calculated values of extinction
coefficient which are plotted on the logarithmic scales, and this re-
lationship can be expressed by the following formula :

$$\log \alpha = 0.40 \; \log C - 0.37 \; \text{-------} \qquad (3)$$

in which C is the mean chlorophyll content of euphotic zone in mg. per m^3.

The fluctuation of incident light intensity during the circulation
period may be regarded to vary according to the daily march as shown in

Fig. 12, which is similar to the monthly average in the light intensity from April to May in Tokyo (Hirayama, 1938). If the loss of incident light by the reflection at the water surface is neglected, it is easy to calculate the light intensity at any time of the day and at any depth of lake water containing a certain amount of chlorophyll by using the equation (1) and (3) and Fig. 12.

To obtain some informations on the quantitative relation between the photosynthetic rate of phytoplankton and light intensity, the photosynthesis of Chlorella cultured under various conditions and of t-he natural algal population taken from various //////////// waters was measured. The results obtained were plotted against light intensity in the relative value, as similar to Ryther's attempt (1956)(Fig. 13). The light saturation of photosynthesis is attained at 1-1.5 x 10^4 lux and the inhibition becomes apparent under the light intensity stronger than 3 x 10^4 lux. In the old aged or less nutrient supplying culture, saturation is observed in lower light intensity and more marked inhibition in stronger light intensity. As the experimental data are insufficient to determine the photosynthesis-light intensity curve of algae under different culture conditions, a tentative curve shown in Fig. 13 was performed as a standard photosynthesis-light intensity surve. This curve seems approximately similar to those given by Manning and Juday (1942) and by Ryther (1956).

The ratio of respiration loss to the maximum photosynthesis also markedly varies with the difference in the age and the nutrient condition. The present experiment in cultured Chlorella showed that the ratio varies within the range of 1/40 to 1/2, and that the algae cultured in a low nutrient level has smaller ratio (cf. Ryther, 1954; Kok, 1951). As the data obtained were not sufficient to reveal the quantitative relationship between the maximum photosynthesis and respiration, it was assumed that the amount of the latter equaled to 1/12 of the former irrespective of the environmental conditions.

Based on the data mentioned above, one can calculate the photosynthetic rate at any depth in a water column, and the total photosynthetic rate of phytoplankton community under the unit surface area. Fig. 14 shows the relation of the relative daily rate (Kr) of the integrated photosynthesis per unit depth of water column to the product of extinction coefficient and water depth (αD). With the increase of αD, the magnitude of Kr decreases due to the lowering of the average light intensity resulting from the increase of mutual shading in the phytoplankton community.

To obtain the absolute value of the daily photosynthetic rate, it is necessary here to multiply this relative value by the photosynthetic rate under the saturation light intensity. Fig. 15 shows the relation between the photosynthetic rate (Pm) of various natural phytoplankton populations measured under the artificial illumination of about 20 kilo lux and the phosphorus level of the sampled waters. It is clear from comparison of this curve with a straight line in Fig. 10 that the photosynthetic activity per unit chlorophyll amount decreases with the lowering of the nutrient level (Ichimura, 1957).

Thus, one can compute the absolute integrated photosynthetic rate (P) of phytoplankton community in the waters having various depths by the following equation :

$$P = Kr \times Pm \times D \quad - - - - - - - - - - \quad (4)$$

Now, suppose here that the growth of the phytoplankton community in the water column concerned is restricted only by less supply of nutrient salts. The amount of phytoplankton given in Fig. 10 seems to be approximately equal to the maximum yield. In consequence, the value of   under a given nutrient level will be obtained from Fig. 10 and 11, and the value of Kr for the water column of a difinite depth from the curve in Fig. 14. Then, using the equation (4) and the data in Fig. 15, the net production rate in the water column of 1, 2, 5, 10 and 20 m. depth can be calculated respectively.

The results were shown in Fig. 16 in mg. of the assimilate (CH_2O).
In this case, the photosynthetic quotient was assumed to be 1. In the
waters of a lower nutrient level, the production rate per unit surface
area is roughly proportinal to the depth of water column. This indicates
that the production in these waters is mainly limited by the amount of
nutrient salts in the lake waters. With the increase in the nutrient
level, the production rate becomes larger. However, the increasing gradi-
ent in production rate with the increase in nutrient level becomes gra-
dually small. Such tendency of variation in the production rate becomes
marked with the increase in the water depth. This indicates that the
photosynthetic rate of the community becomes smaller due to the increase
in the ~~photosy~~ mutual shading degree with the increase in depth and
nutrient level. Thus, the water depth which gives the largest production
rate becomes gradually shallower with the increase in nutrient level.
The absolute values of the net production given in Fig. 16 were obtained
from the calculation based on the value of Pm measured at 20-25° C. As
the water temperature during vernal and autumnal circulation periods is
usually 4-15°C, the actual rate may be about 30 % lower than the present
ones.

The calculated total production rate of too dense phytoplankton
community falls to zero under definite nutrient levels. This suggestes
that the growth of phytoplankton under those conditions is limited pre-
dominantly by the light condition in the water column concerned. It appears
that phytoplankton can not increase beyond certain density. This definite
density may be regarded as the maximum yield (Yml)[*] which can be expfected
from light conditions prevailing in the lake ~~conditions~~ concerned. As

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[*] The maximum yield in the natural waters equals to the size of the communi-
ty in which the production rate is equilibrated with loss rate. However,
as the loss rate during the growing season such as circulation period is
small, the value of Yml may be regarded as an approximation of the actual
one.

clearly seen from the equation (4), P becomes to zero when Kr is zero. Fig. 14 indicates that Kr becomes to zero when D is 19.75. Then, if the depth of lake (D) is known, the maximum yield (Yml) of phytoplankton community can be computed from the equation α = 19.75 / D and the data in Fig. 11.

A solid line in Fig. 17 shows the relation of the computed Yml to the lake depth. It is clear that the shallower the lake is, the larger the value of Yml to be attained. Broken lines in Fig. 17, which were given by the data in Fig. 10, represent the maximum yield of phytoplankton under sufficient light condition and the phosphorus level shown by the figures in parenthsis. It must be kept in mind here that in the water of phosphorus level shown by the figures in parenthesis phytoplankton cannot increase over the broken and straight lines which are bordered with fine oblique lines in this figure. It is clear that the yield of phytoplankton community in the lakes of lower untrient level except the deepest one is restricted by the less supply of nutrient salts, but in the lakes of higher nutrient level it becomes rather influenced by the decrease of light intensity with the increase in lake depth than by the amount of nutrient salts.

According to the author's theoretical computation based on the photosynthesis-light intensity curve of Chlorella (Tamiya et al., 1948, 1953), the result of which will be reported in detail in another paper, the difference in temperature appears to have a large effect on the production of phytoplankton community only in lower density, but not in higher one. Then, for the simplification of the consideration it may be assumed here that the difference in temperature have no substancial effect on the maximum yield of phytoplankton community.

As described before, the amount of phytoplankton observed in the natural waters during a circulation period may be regarded as approximating to the maximum amount to be attainable under the prevailed conditions for that period. Therefore, the quantitative relationship be-

tween the lake depth and the size of phytoplankton community during this period may be explained by the present theoretical relationship. In Fig. 18, a solid line expressing the relationships between Yml and D is identical with the theoretical one shown in Fig. 17. The broken line which was calculated from the data in Figs. 10 and 5-A, represents the relation between the lake depth and the maximum yield expected when the growth is limited only by the nutrient condition. Hence, both broken and solid lines in Fig. 18 bordered with fine oblique lines express the theoretical relationship between the maximum yield and the mean depth during a circularion period in Japanese lakes.

The theoretical values of the yield (chlorophyll mg. per m^3) agree well with the actual ones (open circles in Fig. 18), althoug some deviation is found in the intermediate depth. As described previously, the ratio of respiration loss to the maximum ohotosynthesis becomes larger in the water of lower nutrient nevel. Then, another values of Yml calculated under the assumption that the respiration loss is 1/6 of the saturated photosynthesis, were shown by fine straight line in relation to the lake depth in Fig. 18. This value agrees well with the observed ones in the lake of intermediate depth, but in the deeper lakes it is lower than the observed one. This may suggest that in deeper lakes the circulation of water during this period is limited only in the layer of about 50-60 m. depth from the surface.

3. Production of Phytoplankton Community during Summer Stagnation
   Period.

In summer stagnation period, the stratification of lake water, especially in deeper lake, can be observed throughout this period. In shallower lakes, however, as the stratification tends to be destroyed by the wind action, the lake water may be considered to be circulating throughout the year, though hot completely. The size of phytoplankton community found in the euphotic zone of deeper oligotrophic or mesotrophic lakes during this period is usually much smaller than that found

in the vernal circulation period (Rodhe, 1956). In shallower eutrophic lakes, the former is usually larger than the latter (Ichimura, 1956). The typical examples of these types in the annual variation of the amount of phytoplankton in the euphotic zone are presented in Fig. 18.

Fig. 20 shows the vertical distribution of phytoplankton in these lakes. It appears evident that there is also the similar pattern in annual variation of chlorophyll in deeper layer to that found in the surface layer. It must be noticed here that in the summer season the chlorophyll content of each layer in deep lake increases with depth. This phenomena has been recognized by many workers and generally explained as a result of the sedimentation of phytoplankton cells which had flourished in the epilimnion (Manning & Juday, 1942; Gessner, 1943; Hogetsu et al., 1953).

It is interesting here to compare such patterns mentioned above with these of limiting nutrient salts as nitrogen and phosphorus. However, the parallel measurements of the total nitrogen or phosphorus content with those of chlorophyll have not been unfortunately undertaken. Then, in the present section, the data measured separately by the author and the other workers will be adopted as the references. Table 1 indicates that in the surface water of shallower eutrophic lake, the total phosphorus or total nitrogen content in the summer season is not smaller but rather larger than that in spring. In deeper mesotrophic or oligotrophic lakes the situations are quite reverse.

Table 4 shows the vertical and seasonal variation in total phosphorus content measured by Hogetsu et al. (1952) in Lake Suwa and by Hanya (1957) in Lake Haruna. It is apparent that in deep Lake Haruna the phosphorus content in summer is always smaller than that in spring,

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* These data were kindly put at the author's disposal by Dr. S. Ichimura, to whom his due gratitude is extended.

especially in the surface layer. In shallow lake Suwa, though clear tendencies on the annual variation can not be obtained immediately from the data in Table 4, the content of total phosphorus in euphotic zone in summer seems to become larger than that in spring, but in deeper layer this tendency becomes reverse.

These phenomena seem to result from different state of water circulation. Namely, in deep stratified lake, phytoplankton which grows in euphotic zone under plentiful supply of nutrient salts and light intensity, after perishing was precipitated to hypolimnion although a part of it is mineralized during its sedimentation. This should be associated with the transport of nutrient salt from epilimnion to hypolimnion. For lack of water circulation, the nutrient salts in hypolimnion can be scarcely recovered to epilimnion, and then euphotic zone becomes gradually more oligotrophic. On the contrary, as the water in shallower lake is frequently stirred, perished and deposited plankton bodies are brought again to euphotic zone and repidly mineralized under higher temperature, resulting in the luxuriant growth of phytoplankton in this layer.

Although quantitative explanation could not been given in the present paper due to insufficient fundamental data, it may be said that the scacity of phytoplankton in deeper lake in summer mainly results from poverty of nutrient salts in the euphotic zone. However, one must pay attention to the fact that the specific nature of phytoplankton community in shallow eutrophic lake is diverse from that in deep oligotrophic lake. While the summer phytoplankton community in the former lake is usually dominated by blue-green algae, that in the latter by diatom. Generally, it has been recognized that under strong light intensity and at high water temperature the photosynthetic activity of diatom languished, but that of blue-green algae contrariwise strengthens (cf. Ichimura, 1957). Therefore, the differences in the inherent nature of phytoplankton must be also responsible for the

difference in the growth of phytoplankton community in summer in both types of lakes.

As far as present data are concerned, it will be reasonable to conclude that the differences in the state of water circulation and regeneration of nutrient salts which depend on the shape of lake basin, produce the difference in the concentration of nutrient salts and the production of plankton substances in the euphotic zone.

4. Quantitative explanation on the close relationship between the lake depth and nutrient salts content in the lake water.

Generally, the content of nutrient salts in lake water is determined by the balance among the following four processes : a) supply of nutrient salts from outside area into the lake, b) loss of available nutrient salts either by the adsorption on the surface of the substratum or by the sedimentation of plankton substances, c) regeneration of the parts contained in plankton, sediments and substratum, and d) loss ~~substance~~ ~~nutrient~~ by outflow of autochtonous plankton substance and nutrient salts from the lake.

In the first place, the supply of nutrient salts into the lake appears to be performed by precipitation on the lake surface, inflow of river, ground waters and other streams from surrounding area, and artificial affairs.

It has been well known that the content of nutrient salts in rain waters is usually very small. According to Miyake and Sugiura (1957) nitrogen content of rain water in Japan is 0.6 ppm. on the average. The author's analytical result shows that phosphorus content in the rain water collected on Mt. Hakone in Middle Japan was about 0.002 ppm. Since the annual precipitation in Japan is 1500 mm. on an average and the evaporation from the lake surface is assumed to be nearly

500 mm. per annum, it may be regarded that the water of 1 m^3 in which

the content of nitrogen and phosphorus are 0.9 and 0.003 ppm., respec-

tively, is given on the lake surface of 1 m^2 per annum. Comparing this

content of nutrient salts, especially phosphorus, with that in river

water is very poor in essential nutrient salts. Therefore, it may be

concluded that the rain water dropping on the lake surface does not

operate as an active supplier of nutrient salts except for extreme

oligotrophic lake.

On the contrary, the river water and other inflowing waters from

the surrounding area are very important as the supplier of nutrient

salts in many lakes. The content of nutrient salts in these waters

are usually influenced largely by geological and geographical charac-

teristics of the drainage basins. In Japan, shallower lakes are loca-

ted on fertile plains, but deeper ones on barren mountain districts.

Yoshimura (1931) mentioned that in lake water the close relationship

between the mean depth and nutrient salts content in lake water may be

partly caused by such situation. The fact that the tropical caldera

lakes are generally eutrophic irrespective of their depth (Ruttner,

1931) cannot be explained logically, unless the active supply of

nutrient salts from surrounding area and the rapid turnover of the

salts under high temperature condition are taken into consideration.

Recently, eutrophication due to human activity has become conspicuous

in many lakes (Edmondson et al., 1957 etc.).

If the content of soluble nutrient salts in the inflowing water

is constant, the supplying rate of nutrient salts into oligotrophic

lake seems to correlate closely with the rate of water inflow. It

must be noticed here that the inflow causes the outflow of lake water

and results in the loss of some parts of nutrient salts and plankton

substances. In consequence, the inflowing water has two important roles

that conflict with each other in nutrient salts economy in lake. This

is of great interest from ecological point of view in the succession of lake and will be discussed in detail in the next paper.

The sedimentation of plankton substances and the regeneration of nutrient salts from sedimenting substances are very important on the economy of nutrient salts in the lake water. As pointed out by many investigators, these processes are largely controlled by the temperature, mechanical mixing state and disolved oxygen content of lake water which are influenced by the shape of the lake basin.

In such a manner, the nutrient salts content of lake water varies markedly by the four processes mentioned above. It is of interest that the lake depth stands in close relation to these processes. In consequence, a change in the lake depth must give a change in the balance between these processes, and consequently, on the nutrient salts economy in the lake water. The annual variation in the nutrient salts content in the lake water is also decided by the change of this balance caused by the seasonal variation of climate. To unearth further the causal relation between the production of phytoplankton community and the lake depth, therefore, it will be demanded to clarify the dependency of these four processes on the lake depth and the climate. It is a matter of regret that detailed investigations on this problem, are still pending.

IV. Effects of Production of Phytoplankton Community on the Accumulation of Nutrient Salts and Shoaling of Lake Basin.

1. General consideration on the factors affecting on the nutrient salts economy in lake waters.

The greater part of plankton substances which have been produced in a lake is precipitated on the bottom surface, makes the lake basin shallower, and produces more eutrophic condition as a result of the accumulation of nutrient salts in undecomposed sediments. Such changes of lake environment affect the production of the plant community

and resuts in the progressive change in quantitative and qualitative characters of the lake biotic community. The ecological succession of lake proceeds under such dynamic mutual actions between the production and the habitat factors such as lake depth, nutrients salts content in the lake water, etc. In the previous chapter, the quantitative studies were carried out on the dependenty of the production of phytoplankton community either on the lake depth of nutrient salts condition. The purpose of the present chapter is to reveal clearly the dependency of nutrients salts accumulation and the change in the shape of lake basin on the production of phytoplankton community and to demonstrate the significance of the dynamic, mutual actions for ecological succession of the lake.

As mentioned before, under oligotrophic condition the production of phytoplankton community is influenced strongly by the amount of nutrient salts in the water rather than the lake depth. The economy of nutrient salts in a lake, therefore, is very important for the production of phytoplankton and consequently on the process of the succession. The amount of nutrient salts in euphotic zone of natural lake is usually determined by the balance between the rates of the following four processes. (i) supply from outside of the lake, (ii) sedimentation of palnkton from epilimnion to hypolimnion, (iii) regeneration of salts from hypolimnion, and (vi) loss by outflow of water to outside of the lake. Conditions affecting these processes must have a large significance on the course of succession in the lake.

The degree of the supply of loss of nutrient salts asociated with the inflow of the river water is determined by the rates of inflow and outflow. As in such a humid temperate region as Japan the surface evaporation of the lake will be usually negligivly small in comparison with the inflow or outflow of water, the inflow rate will be nearly equal to the outflowing rate. Consequently, inflow rate may be regarded as an important measure expressing the degree of supply and loss of the nutrient salts in the lake.

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This situation was already pinted out by Hogetsu and Ichimura in 1953. Carrying out a series of pot culture experiments, they studied on the influence of the inflow of river water and the circulation of lake water on the yield of phytoplankton population and nutrient salts accumulation, and disclosed that the increase of replacing rate always induced the increase of plankton substances and of accumulated nutrient salts under stagnating condition.

2. The relation of replacing rate to the production of phytoplankton community and nutrient salts content in lake waters.

Regarding the influence of the inflow water upon the plankton production in the lake, several works have been carried out in the naturla small lakes of reservoirs in which the diluting effect of the inflow water is remarkable. These works make it evident that when the ratio of the inflow water to the total lake volume was small, a large size of plankton poulation was produced(Brooks & Woodward, 1956).

In the larger natural lakes, however, the influence of the inflow will be probalbly less than that in these small lakes. As the volume of natural lakes differs with each other, the inflow rate should be expresed as per unit volume of the lake for comparative consideration. We shall use here the ratio of the volume of the daily outflow water to total lake volume as a measure expressing the degree of daily supply and loss of nutrient salts or plankton substances, and designate the term for it as "replacing rate" . This measure corresponds to the reciprocal of the "replacement quotient" in the work of Brooks and Woodward(1956). As can be seen from the data reported by Tanaka(1926,1930) and others, the annual mean values of this measure deviate from 0.00002 to 0.025 in the lakes of Japan. In Fig. 21, these values are plotted against annual minimum transparency measured in spring or summer season.

Ichimura (1956) made a report on the curvilinear relation ship between transparency and chlorophyll content in some Japanese lakes. Using his data, a fine curve can be written to express the relation between the replacing rate and annual maximum balue of chlorophull content (Fig. 21). Apparently, the annual maximum values of chlorophyll content become larger with the increase in replacing rate within the range below r = 0.008, but in the range above this value, it show a rapid decrease.

Fig. 22 shows the relation of total nitrogen content (alb.-N + NH$_4$-N + NO$_3$-N + NO$_2$-N) in some Japanese lakes (Yoshimura, 1935) to their replacing rate. This curve is similar to that in Fig. 21, which expresses the relation of chlorophyll content to the replacing rate. This fact indicates the importance of the replacing rate for the economy of nutrient salts in the lake and the production of phytoplankton community. Due attention must be paid h'ere to the fact that the replacing rate is varied markedly by the lake depth which affects the production of phytoplankton community, and that in Japanese lakes the replacing rate becomes smaller with the increase of lake depth (Fig. 23). This may show that the lake depth has some influences on the rate of the supply and loss of nutrient salts besides the influence on sedimentation and decomposition of plankton substances. The lake becomes gradually shallower with the lapse of time in thecourse of succession as a result of sedimentation of suspended substances. It may be said that the depth of lake is the most important factor among various ones which affect the process of ecological succession in the lake.

3. Experimental part.

As the circulating state of lake water differs immensely during the stagnation or circulating period, the effet of inflow of the water on the production of phytoplankton community and on the accumulation of nutrient salts will be greatly diversified in both periods. In order to obtain some information on these effects, two series of model culture experiments were carried out based on the same idea as in the report of Hogetsu and

Ichimüra (1953).

Experiment I. In the first experiment, Chlorella was cultured under the illumination of fluorescent lamps in the medical galss cups of 350ml. capacity. The culture media were prepared by dilution of the basic solution with distilled water to the concentrations of 1/1, 1/6 and1/30% The concentrations of nitrogen and phosphorus in these media correspond to those in hihger eutrophic, mesotrophic and primitive oligotrophic lake waters, respectively(Tab.5). Every day throughout the experimental period, some portionsof the culture media in pots were replaced by fresh media of the same concentration on definite rates with the complete stirring of the culture media. The measuring methods of the algal yield and total phosphorus concentration in the algal suspension are the same as described before.

The time courses of the yield measured once a week are illustrated in Fig.24. It is evident that the growth rate in every series decreases gradually with the passing of time, and in 15 - 20 days after inoculation the algal population reachs to a steady state and its further increase cannot be observed thereafter. In thr culture series of higher replacing rate, the size of algal population at this steady state, mamely the maximum yield, is smaller than that in theseries of lower replacing rate. The difference in the concentration of the culture media appears to give no remarkable ef et on the relation of the population size at the steady state to replacing rte. In the case of lower one, however, the decrease of algal yield, presumably due to the extrem defieit of nutrient salts, occurs after reaching to the steady state. These situations will indicate that the increase of the replacing rate gives more marked diluting effect upon the algal population and induces the reductiof population size in the pots even under every nutrint condition.

In this case, in what degree is the economy of nutrient salts in the pots varied by the replacement of the water ? To answer this question, the content of total phosphorus, which is regareded as a minimum element in the present medium, was measured using the algal suspension cultured under stirring condition and sampled in 19 days after the inoculation. The result shows that in the cultures of the same nutrient level there was no difference of the total phosphorus concentration among the culture series with different replacing rate (Tab. 6), and that these values were equal to those of the fresh medium in each series (Tab.5) . This suggests that under the stirring condition, the outgoing of phosphorus was balanced with the incoming, mamely the phosphorus economy was kept constant throughe out the period concerned. A similar situation of nutrient economy may be also expected in the case of other nutriant salts.

On the other hand, any traces of soluble nitrate-nitrogen(by diphenyle-amime mithod) and phosphate-phosphorus can not be detented in the supernatant of the algal suspension sampled in 19 days after the inoculation. Therefore, it may be said that under sufficient light condition the total amount of nutrient salts bound by the algal population at the steady state is constant independent of the difference of replacing rate, but the content per unit amount of algae becomes lager with the increase in replacing rate.

Experiment II. The method employed here is essentially similar to that in the former experiment exeept for the following modifications. As a culture medium, 1/1 culture solution was used. Partial replacement of the medium was carried out without daily sti ring of the culture medium apart from the stirring in sampling days.

The time course of algal yield in the culture series of lower replacing rate (Fig. 25) are similar to those in the former experiment (Fig.24), but in those of higher replacing rate, the yield continuouily increase

with time. Thus, the relation of the yield to the replacing rate becomes exactly opposite to that in the former experiment (Fig.26). The timely change of the total phosphorus content of the sampled algal suspension and the relation of the content to the replacing rate are shown in Fig.27. and Fig.28, respectively. Apparently, the time course of the total phosphorus content of the sampled algal suspension os very simolar to that of the algal yield(Figs.25 and 26). Since soluble phosphate-phosphorus could hot be detected in the supernatant of the suspension taken in 15 days after inoculation, the situation recognized in Figs.27 and 28 would have to be regarded as having been caused by the production of phytoplankton population. As the algae can grow rapidly with complete exhaustion of supplying nutrient salts under the condition of lower nutrient level, the yield of the algae must be controlled to a certain limit by the supplying rate of nutrirnt salts, consequently by the replacing rate. Algal substances produced in the pots, however, for the lakk of water circulation, is not carried saway with the outflow water but settled down on the bottom of the pots, and results in the gradual increase of nutrient salts content in the pots with time. Proportionality between the replacing rate and accumulation of nutrient salts seems to be caused by such situation.

The results of the two experiments described above can be summarized as follows : When the nutrient salts in the culture medium are conspicuously limiting the growth of algae and the medium is continuously circulating, the increase of the replacing rate always brings about the reduction of population size, but no effect on the nutrient ecomogy in the medium. On the contrary, when the water is stagnating, the increase of the replacing rate induces the accumulation of nutrient salts. In natural waters, the fomer condition may be regarded as approximately coresponding to the state of lake during complete circulation period, and the latter to that of stagnation period. Consequently, the inflow rate of river water and the

circulating state of the water in the epilimnion during summer stagnation period should have the important meanigs on the eutrophication of the lake, and on the successional fate of the lake.

4. Theoretical part.

Described hereafter are the results of the theoretical consideration performed to clarify in what manner and in what degree the production of phytoplankton community, the accumulation of nutrient salts and the shoaling of lake basin are influenced by the lake depth and the inflow rate throughout a seasonal cycle of different water circulations. On the basis of these results, the dymanical relations between the lake depth and the production of phytoplankton community and its significance for ecological succession will be discussed.

For the sake of simplicity of the considerations, the following assumptions are adopted here : The water, its mineral composition being similar to the mean value in Japanese river waters(cf. Kobayashi, 1953), flows into the lake from surrounding area at a constant rate throughout the year except the winter season. In consequence, among major dissolved nutrient salts, phosphorus is predominatingly limiting the growth of phytoplankton, This inflow water is always introduced into the circulating layer of the lake and homogeneously mixed with the water in it. Namely, during vernal circulation period (one month), the inflow water is mixed with the whole lake water. In summer stagnation period (five months), it is introduced into the epilimnion of 5 m. thickness, and in autumnal partial circulation period into the circulating layer whose depth becomes gradually deeper

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* These values are largely varied by the shape of lake basin and the climate. The present values, which may be regarded as mean values for each rate or length of period in Japanese lakes, were obtained from the rports by Yoshimura(1937) and others.

at the rate of 10 m. per month . The supply of nutrient salts into the lake is done only by the inflow water, and not by other matters. On the other hand, the inflow of river water brings about the outflow of lake water with plankton cells and nutrient salts from the circulating layer. During the winter stagnation period (one month), there are no inflow of water and the loss of autochtonous substances owing to the freezing of surface lake water.

Physilogical behavior of phytoplankton living inthelake water is defined as follows : Under the optimum nutrient condition, the yield of phutoplankton population follows the growth curve (Fig. 29) calculated from a photosynthesis-light intensity curve (at $15^{\circ}C$) of Chlorella reported by Tamiya and Chiba (1948), and from light factor which is decided by the extinction coefficient of the lake water and light intensity at the lake surface. When the nutrient salts are limiting, the change of phytoplankton population takes place in conformity with that of nutrient salts concentration, especilly that of phosphorus, in the lake water. The ratio of absorbed phosphorus to the dry weight of the plankton is presumed to be constantly 1 : 100 independently of the difference in enviromental conditions. As the average phosphorus content of river water is 0.01 mg./l (Tab.3), the inflow water sustains the phytoplankton population of 1 mg./l. The daily death rate of living cells during a summer stagnation period and an autumnal partial circulation period is regarded as 2 % and the dead cells settles down at the rate of 20 cm. per day(cf. Hogetsu et al., 1952). Mineralization of perished plankton cells takes place independent of water temperature and proceeds retrogressivlely with time, and after one year only 22 % of them are left in the form of undecomposed sediment(cf. Saijo, 1955).

Now, suppose that here are several lakes of different depth (5-50 m.) and of the same surface area, in(t) which the waters enter from the surrounding at various rates. If, at the begginning of spring, those lake warers contain no sedimenting substances and are similar to the inflowing water in their chenical composition, the growth of phytoplankton population during a vernal circulation period will be controlled primarily by the light factor and mechnical diluting effect of inflowing water. Then, it is evident that the larger the replacing rate is and the deeper the lake depth is, the lesser the growth rate of the population becomes(Fig. 29). As the lake water continuously and completely circulates, the variation of nutrient salts concentration in the lake water does not occur. Then, within one month from the beginning except for the case of very large replacing rate, the growth of phytoplankton becomes limited by the nutrient factor throughout a vernal circulation period, and the standing crop of 1 mg./l is kept constantly under various replacing rates.

In a summer stagnation period, free nutrient salts in the lake water are almost exhausted by the vernal growth of phytoplankton(cf.Odum, 1955). Consequently, the production of phytoplankton community is largely controlled by the inflowing rate, in other words, by the supplying rate of nutrient salts by inflow water. Now, consider the lakes of constant depth, in which the river water is flowing in at different rates. The concentration of nutrient salts (C) at any time in the epilimnion of these lakes can be expressed by the following equation :

$$C = c\left[1 - (1 - \bar{r}_e)^t\right] \quad\text{————————— (1)}$$

where c is the concentration of nutrient salts in the inflow water, r is the replacing rate in epilimnion and t is the time in days.

As the inflow and outflow of the water take place continuously, even for a moment, equation (1) may be transformed into

$$C = c\,(1 - \bar{e}^{rt}) \quad\text{———————————— (2)}$$

The amount of phytoplankton (P') in the epilimnion at any time can be expressed by the following equation derived from equation (2) on the assumption that inflowing water of one liter sustains one mg. of phytoplankton:

$$P' = 1 - e^{\bar{r}_e t} \qquad\qquad (3)$$

Considering the sedimentation of perished phytoplankton, equation (3) can be rewritten as

$$P = \frac{\bar{r}_e}{\bar{r}_e - d}(1 - e^{\bar{r}_e t}) \qquad\qquad (4)$$

where P is the amount of the l i v i n g phytoplankton in the epilimnion at any time and d sedimenting rate of perished plankton cells.

In the earlier stage of its growth, the production rate of the population is not usually high enough to exhaust the nutrient salts supplied, and light is predominatingly limiting the growth of phytoplankton. After the population increases to a certain level, nutrient salts become a limiting factor for it and the increase or decrease of phytoplankton population occurs according to equation (4). If the water exchange in the epilimnion is too large, the loss of produced plankton substances becomes large, and even at the end of this period the growth of phytoplankton would be limited only by the light factor. Then, the amount of phytoplankton in the epilimnion after 5 months can be computed by the equation (4) and the growth curves calculated theoretically under a given replacing rate. The result obtained shows that the yield of phytoplankton in epilimnion at the end of summer stagnation period becomes larger with the increase of the replacing rate, while this relation becomes just the contrary in higher replacing rate above 0.84 (Fig. 30).

When the growth of phytoplankton is exclusively controlled by the nutrient condition, the sedimenting rate (Dd) of dead ones can be given by the following equation derived from equation (4):

$$Dd = \frac{rd}{r + d}\left[1 - e^{(\bar{r}_e + d)t}\right] \qquad\qquad (5)$$

When the growth is only limited by the light factor, the sedimenting rate can be calculated on the basis of the growth curves described with consideration of loss owing to sedimentation and outflow. From the relation of the total amount of sediment calculated in such ways to replacing rate, it is apparent that the total amount of sediments in summer increases in proportion to the replacing rate(Fig. 30).

When the water flows in at a constant rate, the growing condition in the epilimnion of the lakes of various depths will become constant irrespective of lake depth. In consequence, the amounts of living phytoplankton and precipitating dead one at the end of this period are also constant, too.

During the following summer partial circulation period and autumnal complete circulation period, these living and dead planktons in summer were to some extent precipitated and decomposed. By the begginning of the autumnal circulation period, larger portions of them settle down on the bottom of shallower# lakes, but in deeper lakes they remain in the inner side of the water column for the sake of small sedimenting velocity (Hogetsu et al. 1952). In the later case, larger portions of then are lost with outgoing water during this circulation period. Then, at the end of autumn, the relation of the calculated total amount of summer and vernal undecomposed sediment to the replacing rate becomes as shown in Fig. 31.

In parallel with such change, the plankton substances are produced utilizing the nutrient salts either liberated from sediment or supplied by inflowing waters. In this case, the larger the replacing rate is, the greater the losing ratio of the liberating nutrient salts and the supplying ratio of allochtonous nutrient salts becoms. At the end of the autumnal circulation period, therefore, the amount of the suspending phytoplankton (living + dead ones) becomes as shown in Fig. 31.

These suspending phytoplankton and sediments are precipitated and partly decomposed during winter stagnation period. At the beginning of the following vernal circulation period, the relations of the amount of sediment to the lake depth and replacing rate (absolute rate of water inflow) turns out to be as shown in Fig. 32. It is evident hhat the amount of sediment per unit depth becomes larger with the decrease in lake depth and the increase in replacing rate. This may suggest that the shoaling rate becomes larger with decreasing lake depth.

The amount of available nutrient salts liberated during his circulation period is shown in Fig. 33 in relation to lake depth and replacing rate. Considering this relation together with the inverse relation(Fig. 32) between lake depth and the amount of the sediment which liberates available nutrient salts in the following years, it may be said that the shallower the lake becomes, the more the nutrient salts liberated in spring will become gradually abundant.

The changes in the hydro-enviromental condition received in such manner, have to control the production of phutoplankton community in the following year. As shown in Fig.16, the production of phytoplankton community within a circulating water column under unit area becomes larger with increasing nutrient level and with decreasing lake depth. As mentioned before, if the absolute rate of water inflow is constant, the production during summer stagnation period is constant irrespective of lake depth. Consequently, the annual production in a lake should become larger with the increase in the amount of liberated nutrient salts and that of sediment. This results in a more remarkable change in the accumulating rates of undecomposed sediments and nutrient salts. Thus, shoaling and eutrophication of lake will proceed more rapidly with the lapse of time. Ecological succession of the lake takes place under such dynamic mutual

action between the lake environment and the production of phytoplankton community, and acceleratedly procceds with lapes of time. This fairly coincides with the accepted general trend of ecological succession (Lindeman, 1942).

6. Discusion

As illustrated in the above considerations, the accumulation of nutrient salts and undecomposed sediments in the lake is in close relation to the lake depths. This is based on the situation that the production of phytoplankton plays a dominating role in the changing processes of these hydro-environmental conditions. The production of phytoplankton community is largely controlled by the lake depths, because the lake depths affect ṕ not only the vertical stratification of phytoplankton community and the underwater light intensity, but also the incoming and outgoing of nutrient salts in the lake waters. The chose connection between the lake depths and nutrient salt content in the water, therefore, would be naturally expected.

The present theoretical consideration contains some simplified and convient basic assumptions. In consequence, the explanations given in this paper may be tentative apart from the fundamental interrelations among the lake depths, nutrient salt content of the water and the production of phytoplankton community. To present a more logical explanation on the process of natural succession, it is necessary, first of all, to obtain the detailed information on the following problems, which are of significance on the producting process of phytoplankton and the nutrient salt economy in the natural lakes.

1). The inflowing rate is not always constant throughout the year, but shows considerable variations in conformity with the seasonal variation of precipitation. It differs also with the difference in geographical location. A similar situation to this will be expected in the variation of the nutrient salt content in the inflowing waters, too. The influence

of the inflowing water on the production and nutrient salt economy, therefore, must be very diversified with the differences in seasons and locations. This appears to have an important significance on the geographical variations in the rates of production and succession.

2). In natural open lakes, the inflowing water is often not completely mixed with the water in the circulating layer immediately after having been introduced into the lake (Gessner, 1955; Kojima, 1949, 1958). In the case of a lake in which a larger amount of water is � introduced, therefore, it will be unnatural to consider that the inflowing water is mixed homogeneously with the water in the circulating layer. In the lakes in which a slight amount of water is introduced, however, the present trial may be regarded as an approximation.

3). The rates of sedimantation and mineralization of perished phytoplankton are largely controlled by water temperature. This cannot be neglected on consideration of the dependency of nutrient salt economy in the natural lakes on the shape of lake basin. Unfortunately, the analytical studies on this problem have been scarcely carried out to date.

4). In natural waters, some parts of phytoplankton are lost by the predating activity of zooplankton. The excreta of zooplankton are usually simple organic compounds in nature which are easily mineralized during short periods. Several workers have also reported that the mineralizing rates of dead zooplankton are more rapid than those of phytoplankton. These must accelerate the revolving rate of nutrient salts in lakes, and have a large influence on the production of phytoplankton.

In such a way, many problems remain to be solved in the present study. If the further detailed quantitative infoamation are obtained on the dependency of the growth of phytoplankters of various taxonomic groups on light, temperature and nutrient salts (e.g. nitrogen and

phosphorus) conditions, and the competitive relations between rooted aquatic plants and phytoplankton community, it will become possible to explaine the process of ecological succession in quahitative charateristics as well as in quantitative ones.

Summary and Conclusion

Ecological succession of the lake takes place principally under dynamic mutual actions between the production of phytoplankton community and the hydro-environmental conditions (lake depths and nutrient salts content of the water). For clarification of the process of this progressive change, analytical investigations were carried out on the following two problems : the dependency of the production of phytoplankton community on the morphometry of lake, and the effect of the production of the process of eutrophication and the shoaling of lake. Based on the results obtained, a tentative explanation was given an the initial stage of ecological succession of the lake.

(1). During a vernal circulation period, the dependency of the production of phytoplankton community on its environmental factors was investigated as to the Japanese lakes of harmonic type. The results obtained were as follows :

a). An inverse proportionality was found between the mean chlorophyll content in euphotic zone and the mean depth except extremely shallow lakes with luxuriant growth of rooted aquatic plants (Figs. 1 & 2).

b). The contents of total phosphorus, nitrogen and iron of the surface water of the lakes are 0.008 - 0.07, 0.15 - 1.20, and 0.02 -1.1 ppm., respectively. The inverse proportionality was also found between these contents and the mean lake depth (Fig. 5). Considering the minimum requirement of various algae for each element reported by several workers, it becomes evident that the concentration of nitrogen and phosphorus among various elements contained in the lake water, was relatively less abundant.

c). <u>Chlorella</u> sp. was cultured in the medium of various nitrogen and phosphorus levels, and the relations between the yield and nutrient level were investigated. The results suggested that in natural waters phosphorus would be predominatingly limiting the normal growth of plankton algae (Figs. 6 & 8).

d). Direct proportionality was found between chlorophyll content and total phosphorus or total nitrogen content in natural waters sampled from late spring to early autumn (Figs. 9 & 10). From comparison of these direct proportionality with N:P ratio of the water concerned, it was concluded that the limiting effect of phosphorus on the production of phytoplankton in natural waters was stronger than that of nitrogen.

e). Using the photosynthetic curve of fresh water algae (Fig. 13), the formula expressing a relationship between chlorophyll content and extinction coefficient, and direct proportionality between chlorophyll content and phosphorus level, the changes of the maximum rate of daily net production under the condition of various nutrient sevels and lake depths were calculated. The results were graphically described in relation to the phosphorus level of the waters (Fig. 16).

f). The general relations of the maximum phytoplankton yield under the condition of the complete circulation of water to nutrient level and lake depth were graphically illustrated (Fig. 17) based on the data of Fig. 16. This figure showed as in Fig. 16 that the nutrient salts limited the production and yield of phytoplankton except the deepest lake under more oligotrophic condition. But, under more eutrophic condition, the lake depth become usually a limiting factor owing to the increasing degree of mutual shading. Comparison of this theoretical relation with the actual one in Japanese lakes showed good coincidence (Fig. 16).

(2). During summer stagnation period, the amount of chlorophyll in

shallower lake become more abundant than in spring, and it distributed homogeneously in each layer of the water column. In deeper lakes, on the contrary, it was less abundant on an average than in spring and the content in each layer increases with depth to some extent (Figs. 19 & 20). These seasonal and vertical variations in the amount of chlorophyll were approximately parallel with those in the amount of total nitrogen and phosphorus. The yield of phytoplankton in the summer season may be partly controlled by the difference either in the condition of water circulation or regenerating rate of nutrient salt with depth.

(3). The content of available nutrient salts in euphotic zone is determined by the balance between the following four processes : i) supply of them from outside area, ii) transport from epilimnion to hypolimnion with the sedimentation of phytoplankton, iii) regeneration from mud and undecomposed sediments, and iv) loss with the outflow of waters. The relations of these processes to lake depths were discussed.

(4). The "replacing rate" of inflowing waters in natural lakes is an important factor for the determination of supplying and losing rate of nutrient salts. In Japanese lakes, definite correlations were obtained between replacing rate and chlorophyll or nitrogen content in the lake waters (Figs. 21 & 22). It was also found that the replacing rate was largely controlled by the lake depth (Fig. 23).

(5). The influences of the inflowing rate on the accumulation of nutrient salt and the production of algal substances were investigated by means of pot culture experiments of Chlorella. In the series of stirring culture condition, the yield was inversely proportional to the replacing rate (Fig. 24), but nutrient salt content was constant even under different replacing rate. In the series without stirring, the yield and nutrient salt content became large with the increase in replacing rate and with time (Figs. 25, 26, 27 & 28). These results may indicate

that the accumulation of nutrient salts was induced by the sedimentation of phytoplankton borne nutrient salts in high concentration.

(6). The amounts of production and sediments were calculated theoretically throughout a seasonal cycle of different water circulating periods. It was shown that the amount of sediment and liberated nutrient salts(= the concentration of the salts) per unit lake depth in the vernal circulation period in the following year became larger with the decrease in lake depth and the increase in the absolute rate of water inflow(Fig.32 & 33). By consideration of these results together with the situation in which the annual rate of production per unit area becomes larger with the increase in the nutrient level of the water, the rates of shoaling and eutrophication appears to become larger with the lapse of time. Thus, it may be said that the ecological succession of lake acceleratedly proceeds with the passage of year.

(7). The results of this theoretical analysis seem to be useful for the analysis of the ecological succession in natural lakes in spite of some tentative assumptions in the course of this analysis.

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Legends of Figures.

Fig.1. The relationship between mean depth and the average chloropyll content in euphotic zone of various lakes in Japan.

Fig. 2. Logarithmic plot of the relationship between mean depth and the average chlorophyll content in euphotic zone of various lakes in Japan.

Fig. 3. The relation between mean depth and the product of mean depth and average chlorophyll content in euphotic zone of various lakes in Japan.

Fig. 4. Growth curves of Chlorella cultured in the media of different depth under artificial illumination. Numbers on graph express the depth of the medium in cm.

Fig. 5. The relations of the total-nitrogen, -phosphorus and-iron contents in the various lake waters in Japan to the mean depth.

Fig. 6. The relations between nitrogen level and the yield of Chlorella cultured in the media with varing concentration of nitrate and phosphate for 53 days. Broken lines and figures in parentheses denote the upper and the lower limit of N : P ratio in the natural waters.

Fig. 7. Relation between N : P ratio and phosphorus level in natural lake waters during a circulation period. Dubble circles denote that in river waters; filled circle, that in the water of the shallower eutrophic lakes in which the bloom of Microcystis is produced in midsummer of the rooted aquatic plants are luxuriantly growing.

Fig. 8. The relations between phosphorus level and the yield of Chlorella cultured in the medium with varying concentration of nitrate and phosphate for 53 days. See the legend of Fig.5.

Fig. 9. The relationship between total nitrogen content and chlorophyll

content in the surface waters of various lakes and ponds during a period

from May to September. Figures on graph express N : P ratio of the sampled

waters. Dubble circles denote the value obtained in midsummer.

◑ , obtained in the water in which dominant species was <u>Asterionella</u>

 <u>formosa</u>.; ◐., <u>Melosira</u> sp.; ◓ , <u>Synedra</u> sp.; ◉, <u>Microcystis</u> <u>aureus</u> ;

 ○, Other species.

Fig. 10. The relationship between total phosphorus content and chlorophyll

content in the surface waters of various lakes and ponds during a period

from May to September. For symboles, see the explanation of Figure 9.

Fig. 11. The relationship between the computed extinction coefficient

and mean chlorophyll content in the euphotic zone of some Japanese lakes.

Fig. 12. The daily march of solar radiation. See text.

Fig. 13. A standard photosynthesis-light intensity curve of fresh water

algae.   ⊙ - Chlorella .   x - natural population.

Fig. 14. The relative daily rate (Kr) of total integrated photosynthesis

per unit depth of water column as a function of ⊄D. The arrow shows

the value of ⊄D in which respiration and photosynthesis are equilibrated.

Fig. 15. The relationship between photosynthetic rate under saturated

light intensity and phosphorus level of the water taken from various

lakes and poods. Water temperature at measurement, 22 -25°C.

Fig. 16. The calculated daily rate of total production throughout the

the water column of various depth and different phosphorus level.

Fig. 17 The relationship between the theoretical maximum yield of

phytoplankton community, lake depth and the phosphorus level of waters.

Fig. 18. Comparision between chlorophyll content of various Japanese

lake waters for a circulation period and the theoretical maximum yield

of phytoplankton community.

Fig. 19.   The annual variations of chlorophyll content in the euphotic
zone of a shallower eutrophic lake (Kasumigaur, 1957) and a deeper meso-
trophic lake (Lake Haruna, 1958). Mean depth of the former and the later
are 3.3 m. and 7.9 m., respectively.

Fig. 20.   Vertical distributions of chlorophyll in Lake Haruna (upper figure)
and in Kasumigaura (lower figure). Data were obtained in 1958 in the
case of the former and in 1957 in the case of the latter except for
underlined data in 1956.

Fig. 21.   The relations of the annual minimum values of transparency
and the corresponding chlorophyll content in Japanese harmonic lakes
to replacing rate.   Solid line - transparency ; fine line - chlorophyll
content.

Fig. 22.   The relation of nitrogen content in Japanese lake waters,
measured by Yoshimura (1931), to replacing rate.

Fig. 23.   The relation between replacing rate and mean depth of the
harmonic lakes in Japan.

Fig. 24.   Growth curves of <u>Chlorella</u> cultured under artificial illuminations
in the culture media of dilution degree shown by fractions on the right
side of graph. Every day throughout an experimental period, all cultures
were complesely stirred. ●, Control cultures without water replacement.
×, ○, △, Cultures whose replacing rate were 0.01, 0.02 and 0.1,
respectively.

Fig. 25.   Change of apparent yield with time.   Cultures were not stirred
throughout an experimental period except sampling days.   ● , Control
cultures without treatment of water replacement.   × , ○, △, ◎, Cultures
whose replacing rate were 0.002, 0.01, 0.1 and 0,2, respectively.

Fig. 26.   Change of apparent yield at 21 days after inoculation with

varying replacing rate.   Solid line shows the stirring cultures and fine

line the nonstirring cultures carried out in parallel with the former.

Fig. 27.   Change of total phosphorus content of nonstirring culture with

time. Menanings of symbols are the same to those of Fig. 25.

Fig. 28.   Change of total phosphorus content of nonstirring culture with

varying replacing rate. Figures on graph represent time in day after

inoculations.

Fig. 29.   Theoretical growth curves of Chlorella. Initial amount of alga

was presumed being 0.01 mg/l. and calculated using a photosynthesis-

light intensity curve of Chlorella(Tamiya & Chiba 1943), extinction

coefficient of the water and the date of solar radiation shown in Fig. 12.

Solid line - water coumn of 5 m. depth; Broken line - that of 20 m.depth;

Dotted line - that of 50 m. depth.

Fig. 30.   The amount of living phytoplankton in the epilimnion (solid line)

and precipitating phytoplankton(dotted line) at the end of summer stagnation

period.

Fig. 31.   The relations of the amount of suspending phytoplankton (solid

line) and undecomposed sediment (dotted line) at the end of autumnal

complete circulation period to replacing rate. Figures on graph indicate

depth of lake in m.

Fig. 32.   The relation of the amount of undecomposed sediment at the beginning

of the following vernal circulation period to replacing rate and depth

of lake.

Fig. 33.   The relation of the amount of newly liberated nutrient salts

in the following vernal circulation period to replacing rate and lake

depth.   The amount of nutrient salts was expressed as the amount of phyto-

plankton grown with exhaustion of those nutrient salts.

Table I. The morphometry of various lakes in Japan and the amounts of the containing major nutrient salts, in the surface waters.

Lakes	Altitude (m)	Area (Km²)	Mean depth (m)	Date	Contents of nutrient salts (p.p.m.)				Lake-type
					Total-N	Total-P	Total-Fe	N:P ratio	
Teganuma	3	10.0	1.0	May 16, 1958	1.088	0.041	0.647	26.3	Eutrophic
				Aug. 11, 1958	0.421	0.010	——	39.4	
Kitaura	1	78.8	1.6	May 16, 1957	——	0.092	——	——	
Kasumigaura	1	178.0	3.3	Sep. 16,1956	1.400	0.060	——	23.3	
				Nov. 23, 1956	1.260	0.047	——	26.7	
				May 16, 1957	1.208	0.043	——	28.3	
Suwa	759	14.5	4.1	Sep. 1949	——	0.080	——	——	
				Feb. 1950	——	0.060	——	——	
				May 5, 1958	1.164	0.075	0.542	15.4	
Nakatuna	815	0.14	5.7	May 4, 1958	0.313	0.022	0.252	14.1	Mesotrophic
				Dec. 1958	0.159	0.013	——	12.2	
Syôji	896	0.65	6.7	May 4, 1958	0.435	0.024	0.206	17.9	
Haruna	1.084	1.23	7.9	April 16, 1958	0.365	0.024	0.106	15.6	
				Dec. 1958	——	0.021	——	12.2	
Yamanaka	982	6.5	9.0	May 4, 1958	0.437	0.031	0.208	15.5	
Kizaki	764	1.6	17.9	May 1958	0.259	0.019	0.183	13.5	
				Dec. 1958	0.193	0.012	——	16.5	
Ashinoko	723	6.9	26.4	June 22, 1958	0.224	0.009	——	24.4	Oligotrophic
				Aug. 4,1958	0.044	0.004	——	12.5	
Aoki	822	1.9	29.0	May 1958	0.191	0.014	0.289	13.4	
				Dec. 1958	0.167	0.009	——	18.5	
Motosu	902	4.9	65.3	May 4, 1958	0.162	0.011	0.138	14.9	
Masyû	351	20.0	137.5	June, 1958	0.153	0.008	0.024	19.8	

Table II. Minimum requirement of various planktonic algae for different mineral element in p.p.m.

Species	Investigators	N	P	Fe	Ca	Mg	SiO₂
Pediasurum Boryanus	Chu (1942)	2.1	0.09	0.02	0.20	2.40	2
Staurastrum paradoxum	"	2.0	0.10	—	0.2	4.0	—
Botryococcus Braunii	"	1.4	0.09	—	0.02	0.00	0.04
Nitzschia apalea	"	5.0	0.20	—	0.9	0.1	9.8
Fragilaria crotonensis	"	1.7	0.20	—	0.02	0.1	19.6
Asterionella gracillima	"	1.7	0.18	—	0.18	0.01	9.8
Tabellaria flocculosa	"	—	0.20	—	10.0	1.0	2.0
Ankistrodesmus falcatus	Rodhe (1948)	5.0	0.20	0.04	—	0.1	4.6
Scenedesmus quadricauda	Österlind (1949)	10.0	0.5	0.05	2	2	—
Coccochloris Peniocystis	Gerloff et al.(1950)	13.6	0.45	0.03	—	0.13	—
Microcystis aureus	" (1952)	6.8	0.45	0.06	0.25	2.5	—

Table III. Contents of important mineral elements in the natural freshwaters in Japan, in p.p.m.

	N	P	Fe	Ca	Mg	K	SiO$_2$
Salmonid lake waters by Yoshimura (1936)	0.05-2.0	0.005-0.50	0.001-2	3 -20	1 -5	1 -5	10-50
Normal river waters by Kobayashi et al. (1953)	0.05-1.1	0.002-0.05	—	2.4-28.0	0.4-8.0	0.3-5.9	3-23
	(0.3)	(0.01)	—	(10)	(2.9)	(1.2)	(7.8)

Figures in parentheses express the mean value of the content in the river waters.

Table IV. Vertical and seasonal variations in the total phosphorus
content in the waters of Lake Haruna (mesotrophic, mean depth-7.9m.)
and Lake Suwa (eutrophic, mean depth - 4 m.).

Lake Haruna from Hanya (1957)

Depth in meter	July 18,1950.	Aug.31,1950.	Feb.3,1951.	April 25,1951.
			(p.p.m.)	
0	0.014	0.014	0.035	0.080
2	0.016	0.014	0.035	0.090
4	0.018	0.016	——	0.080
5	——	——	0.035	——
6	0.026	0.018	——	0.080
8	0.025	0.032	0.040	0.080
10	0.028	0.075	——	0.080
12	0.140	0.150	0.030	0.090

Lake Suwa from Hogetsu(1952)

Depth in meter	Sep. 1949.	Feb.1950.
0	0.080	0.060
1	0.080	0.060
2	0.100	0.080
3	0.080	0.050
4	0.010	0.075
5	0.010	0.080
6	0.020	0.065

Table V.   The concentration of major elements in the culture
media in p.p.m.

Dilution degree of the basic medium	1/1	1/6	1/30
Nitrogen	2.770	0.461	0.092
Phosphorus	0.228	0.038	0.008
Ferrous	0.090	0.015	0.003
Calcium	0.361	0.060	0.012
Magnecium	0.987	0.164	0.033

Table Vl.   Total phosphorus concentration (in p.p.m.) of
algal suspension sampled at 19 days after inoculation.

Dilution degree of the basic medium / replacing rate	1/1	1/6	1/30
0	0.250	0.034	0.008
0.01	0.250	0.035	0.008
0.10	0.248	0.029	0.008

　湖沼における生態遷移は、その基本に於て
は植物プランクトン群落の生産と生育環境(湖
の深さと栄養塩類含量)との動的相互作用の過
程に於てあさる。この遷移の過程を明らかに
する為に二つの事項,即ちⅠ.湖盆形態の植物
プランクトン群落の生産に対する支配関係,
Ⅱ.生産の湖盆浅化や富栄養化への作用。に
つき解析的研究が行なわれた。

　1.　(a)循環期に於ける植物プランクトン群
落の生産量と環境要因の関係が調べられた。
　i)平均深度と euphotic zone の平均葉緑素含量
の間に双曲線的比例関係が認められた。この
時の表層水中の全燐、全窒素、全鉄含量と平
均深度との間にも、夫々同様な逆比例関係を
認めた。種々の浮遊性藻類の塩類最少要求量
の資料や chlorella の培養実験の結果は一般の湖
沼ではこれら栄養塩類のうち、燐が特に藻数
の正常生育に不足することを示した。
　ii)種々な湖の表層水に含まれる葉緑素量
と全燐、又全窒素量の間に直線関係が認めら

れた。これと試水の N/P比との比較より、実際の湖水では、特に燐が藻数の生育制限にあづかっていることが明らかにされた。

iii) 種々な深さの水柱につき理論的な植物性プランクトンの純生産力、及び収量の燐酸含量に対する関係が算去され、次のるが明らかになった。貧栄養的條件下では、植物プランクトンの生産や収量は深湖を除けば"栄養塩数量により支配される。栄養度が上るとプランクトンの相互被陰度が増加し、生産や収量は湖深によりより強く制限される様になる。

(b) 夏期停滞期には、植物プランクトン量は深い中栄養及び貧栄養では春より減少するが、浅い富栄養湖では逆に増加する。水中の全燐、全窒素含量も同様の変化を示す。この結果より夏期における生産は栄養塩数の不足で先が制限を受けるるが考えられる。

Ⅱ. i) 湖での塩数の供給あるいは流失の度を表す為、置換率 (Replacing Rate)(r̄) が採用された。日本の湖沼では r̄ の値と、透明度、

窒素含量の間に比例関係がみられた。又この
比は湖の深さで大きく変化する事が知られた.

ii) Chlorella の培養実験により $\bar{r}$ の収量及び塩
類経済に対する関係がしらべられた。攪拌条
件下では $\bar{r}$ の増大は常に収量の低下を招いた
が、塩類の収支は常に一定に保たれた。非攪
拌条件下では、$\bar{r}$ の増大は容器内での収量の
増加及び塩類量の蓄積を招いた。湖沼では、
前者は循環期の、後者は停滞期の条件にみた
ると思われる。

iii) 生産量、沈澱量, 遊離塩類量が一年を通
じて理論的に算出された. 一年後の春期循環
期に於けるそれらの量は $\bar{r}$ の大きい程、湖の
浅い程大きくなる. 年間生産量は栄養度が高
くなる程、又湖が浅さなと程大きくなる関係
と併せ考えるならば、湖の生態遷移は「植物プ
ランクトン群落の生産」と「湖盆の形態」間の動的
相互作用の下で大きり、時間と共に加速度的
にすすむと言える。これは湖沼における遷移
の過程とよく一致する。

<u>Figures</u>
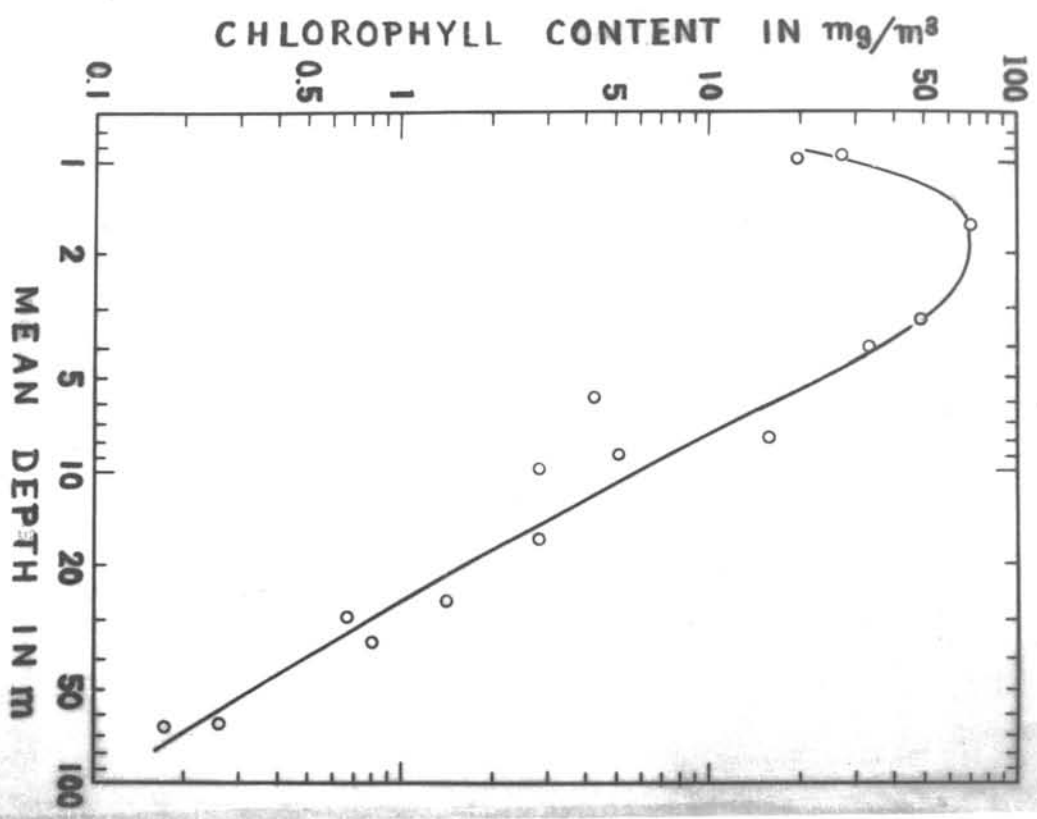
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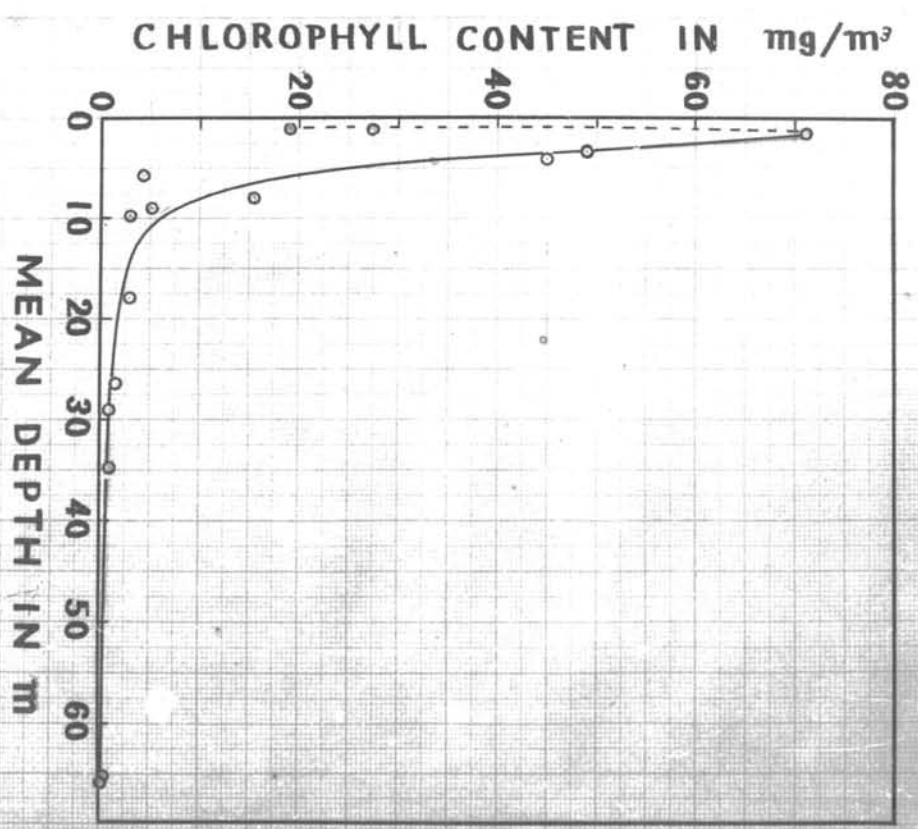
Fig. 1

Fig. 3
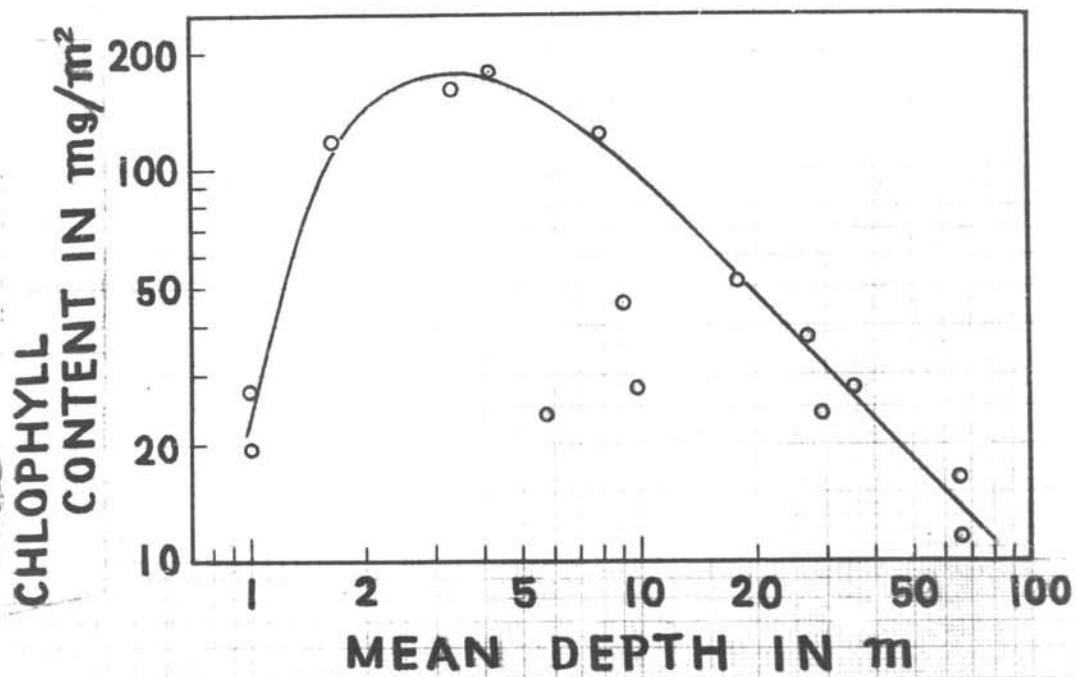
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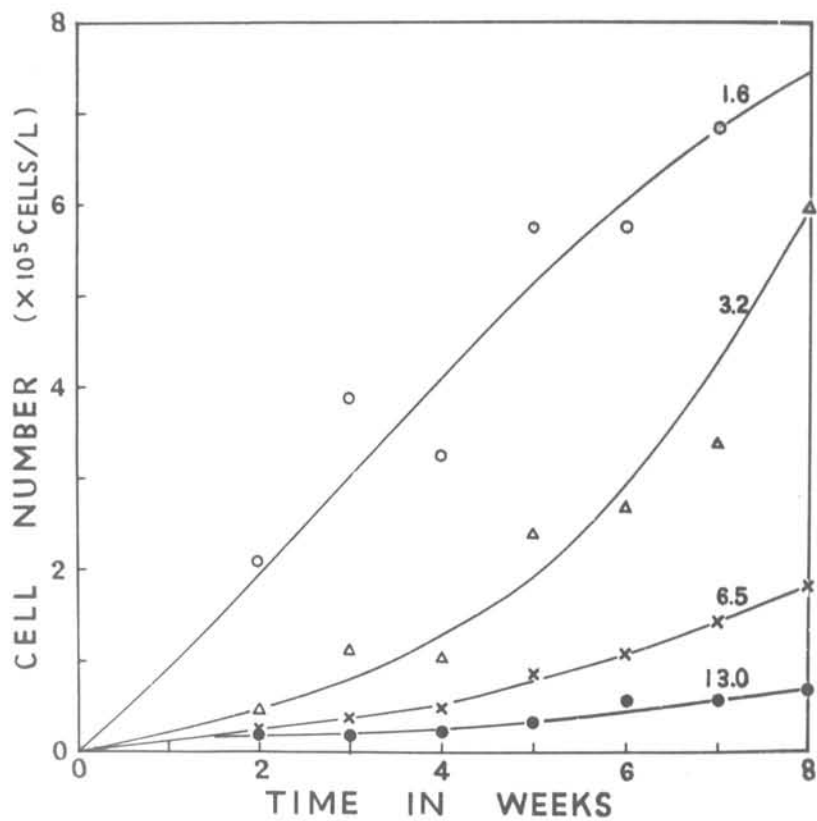
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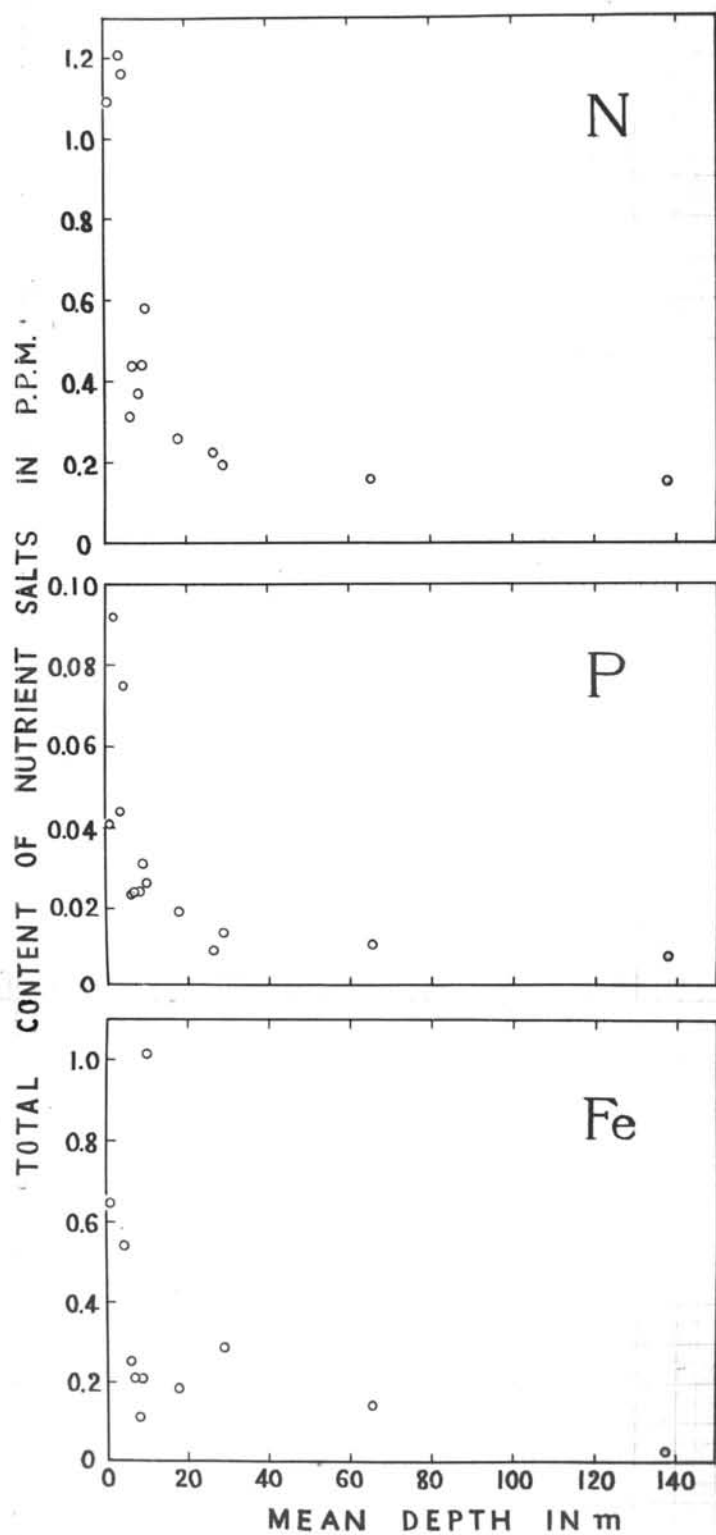
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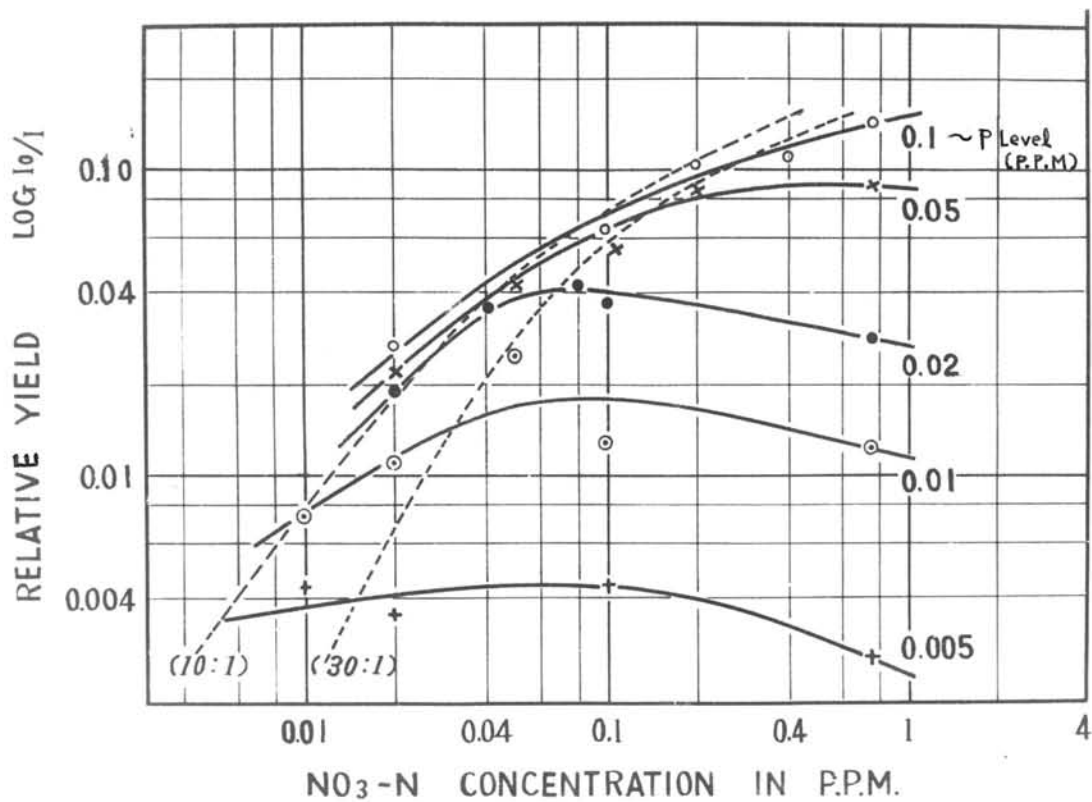
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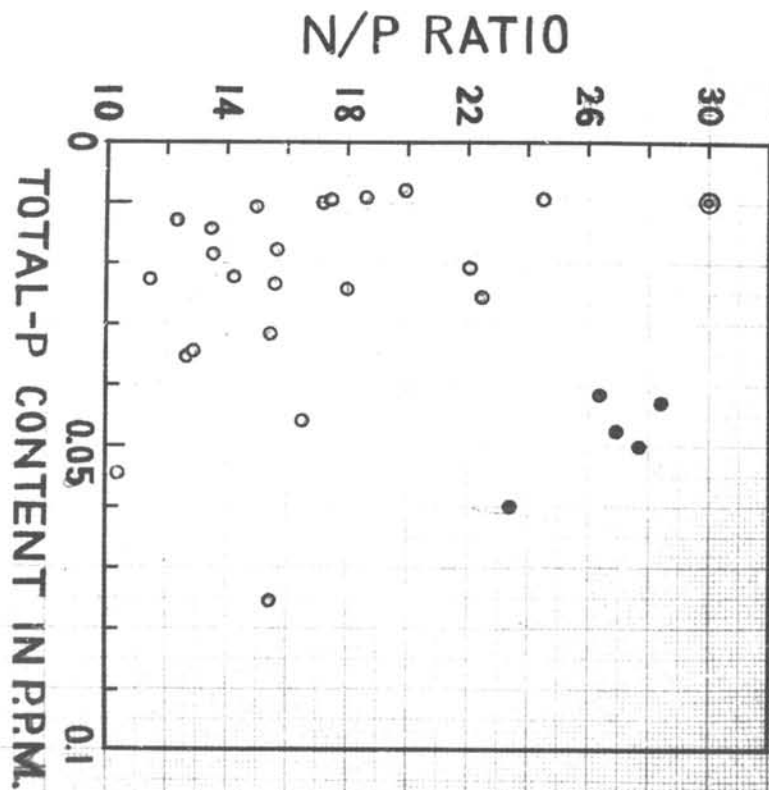
Fig. 8

Fig. 9

Fig. 10

Fig. 11

INCIDENT LIGHT INTENSITY (×10⁴ LUX)

TIME OF DAY IN HOURS

REL. RATE OF PHOTOSYN.

LIGHT INTENSITY   10⁴ LUX

Fig. 14

MAXIMAM RATE OF PHOTOSYNTHESIS (Pm) O_2 mg/L/HR

PHOSPHORUS LEVEL OF WATER, P.P.M.

Fig. 15

NET PRODUCTION CH₂O mg/m²/DAY

PHOSPHORUS LEVEL OF WATER, P.P.M.

Fig. 76

MAXIMAM YIELD OF PHYTOPLANKTON CHL.mg/m³

WATER DEPTH IN m

Fig. 77
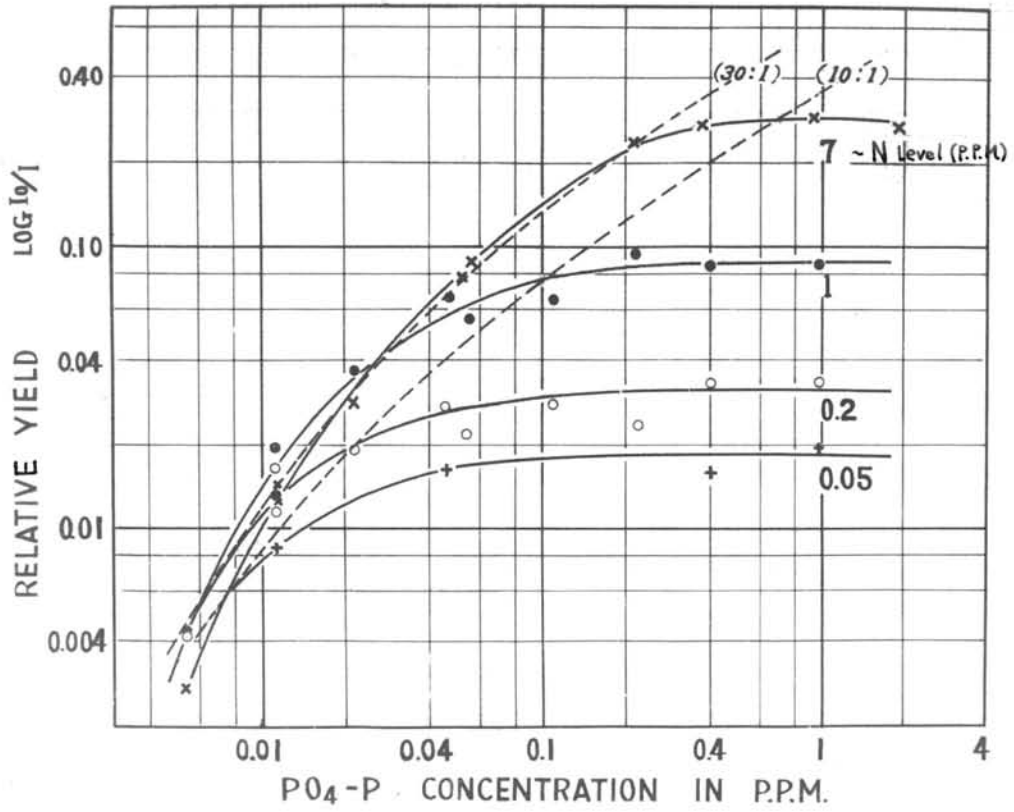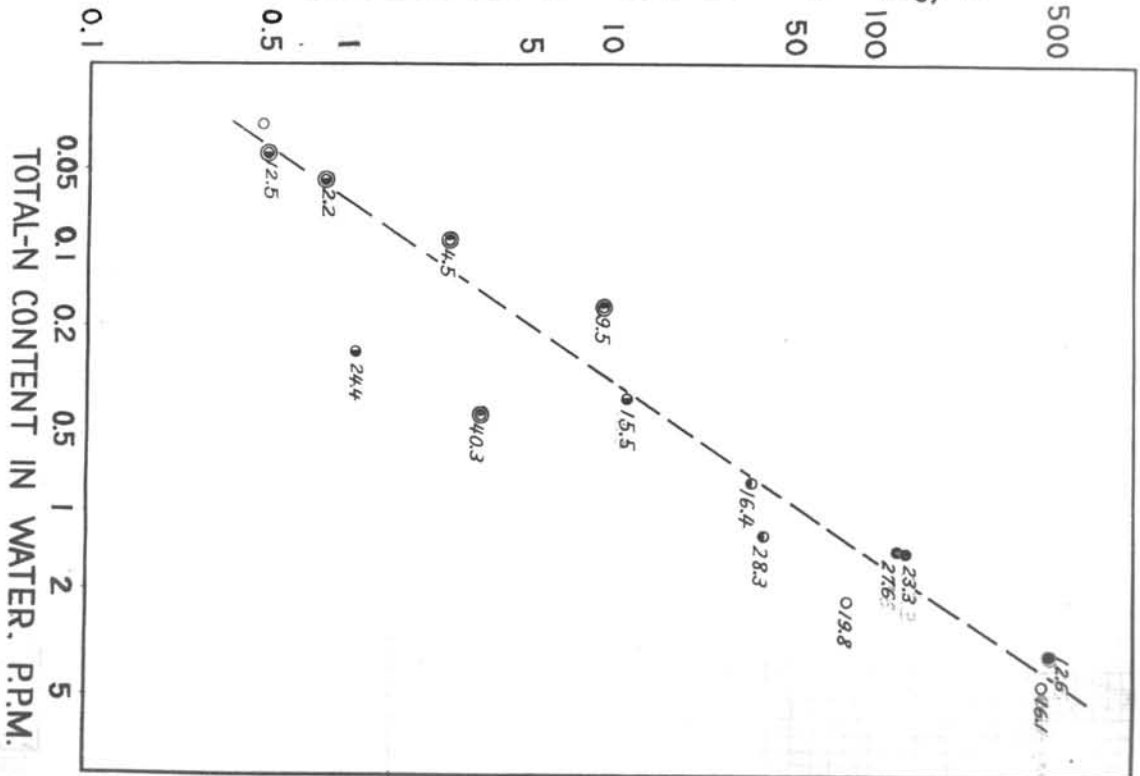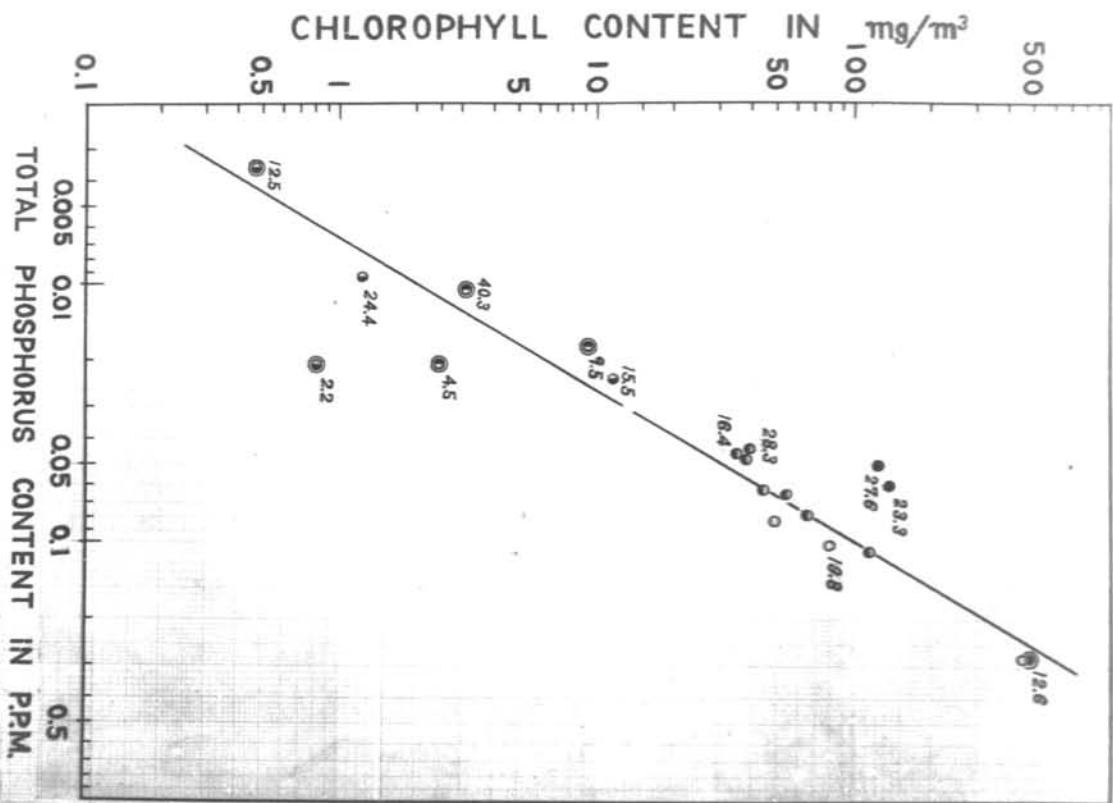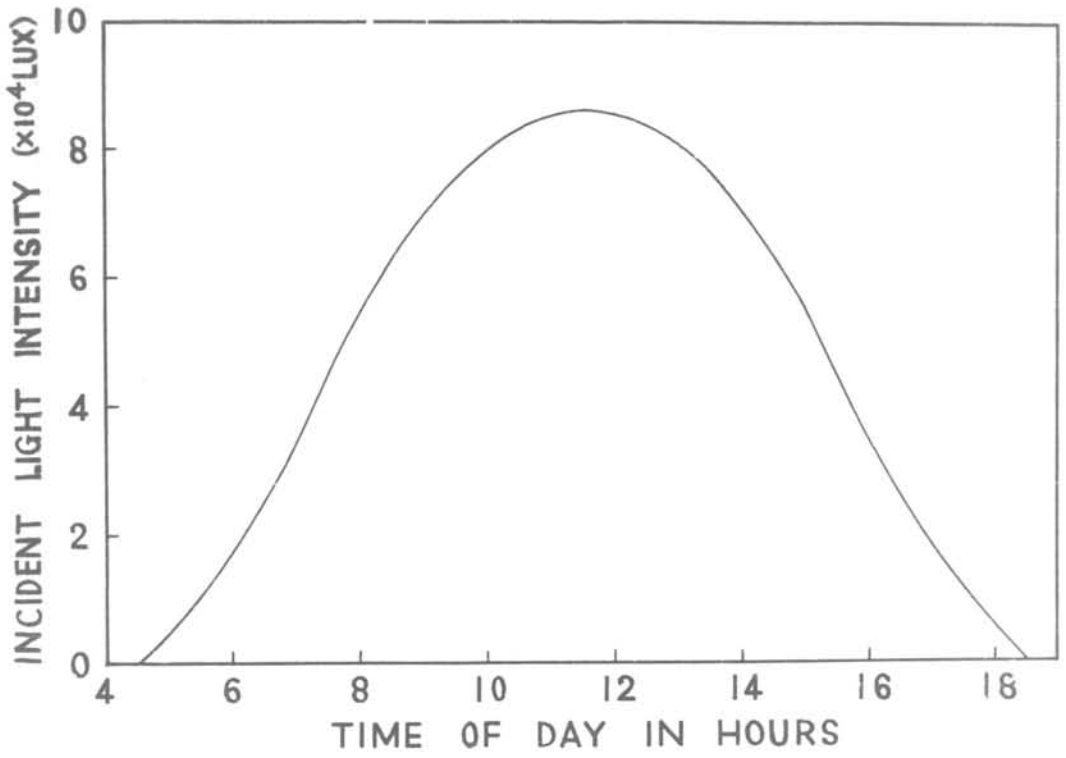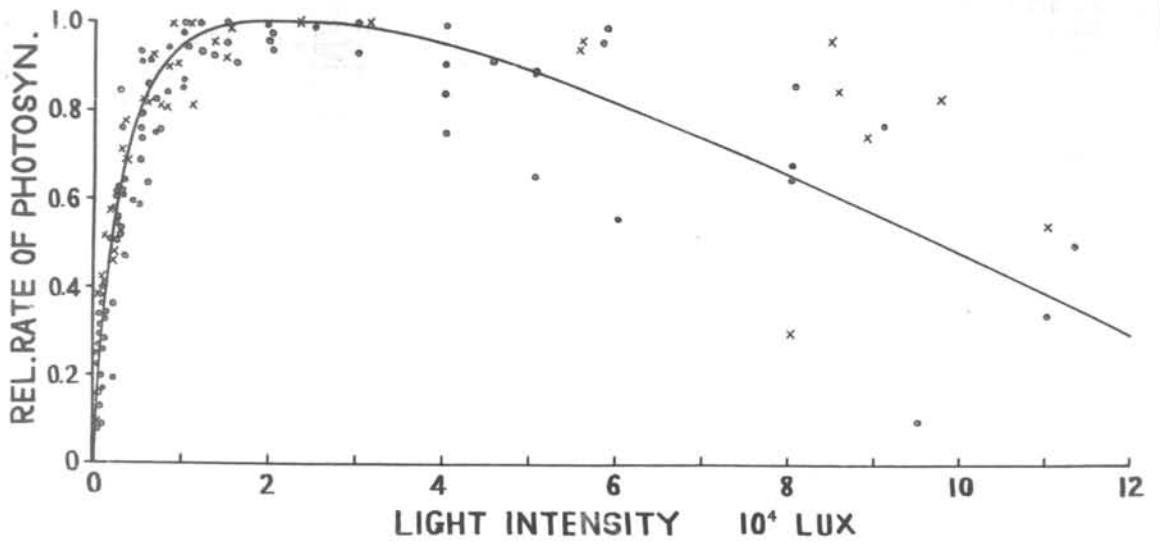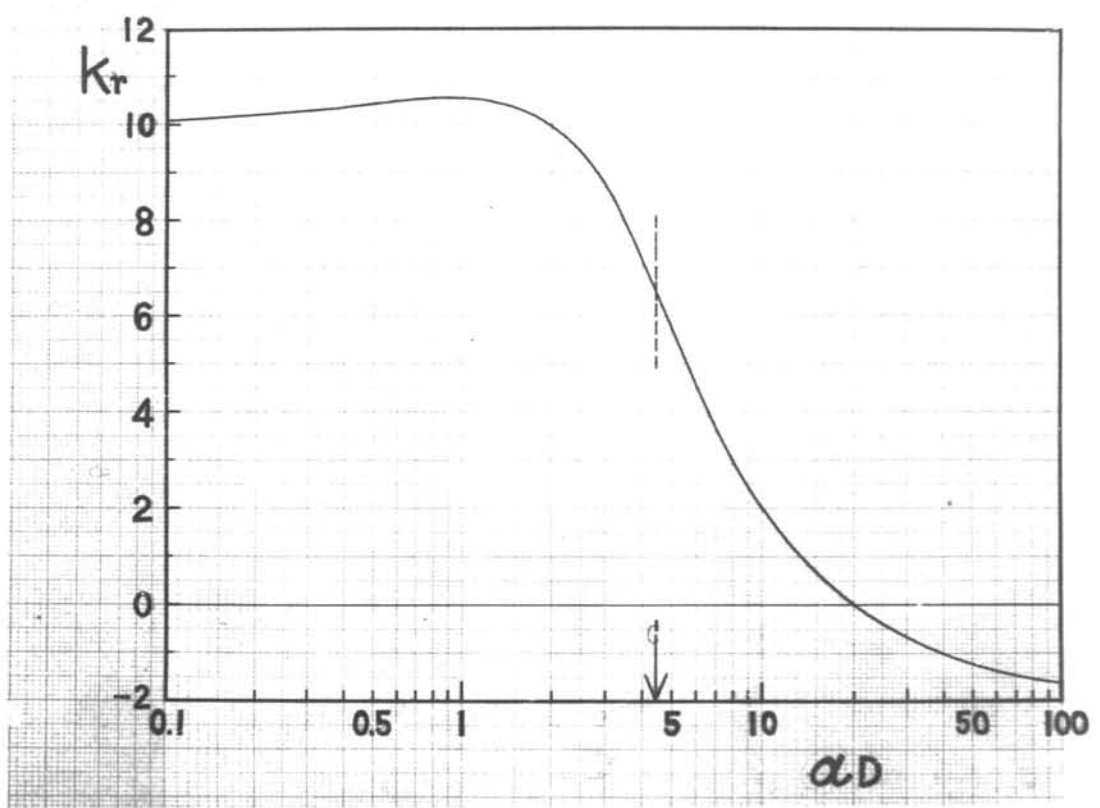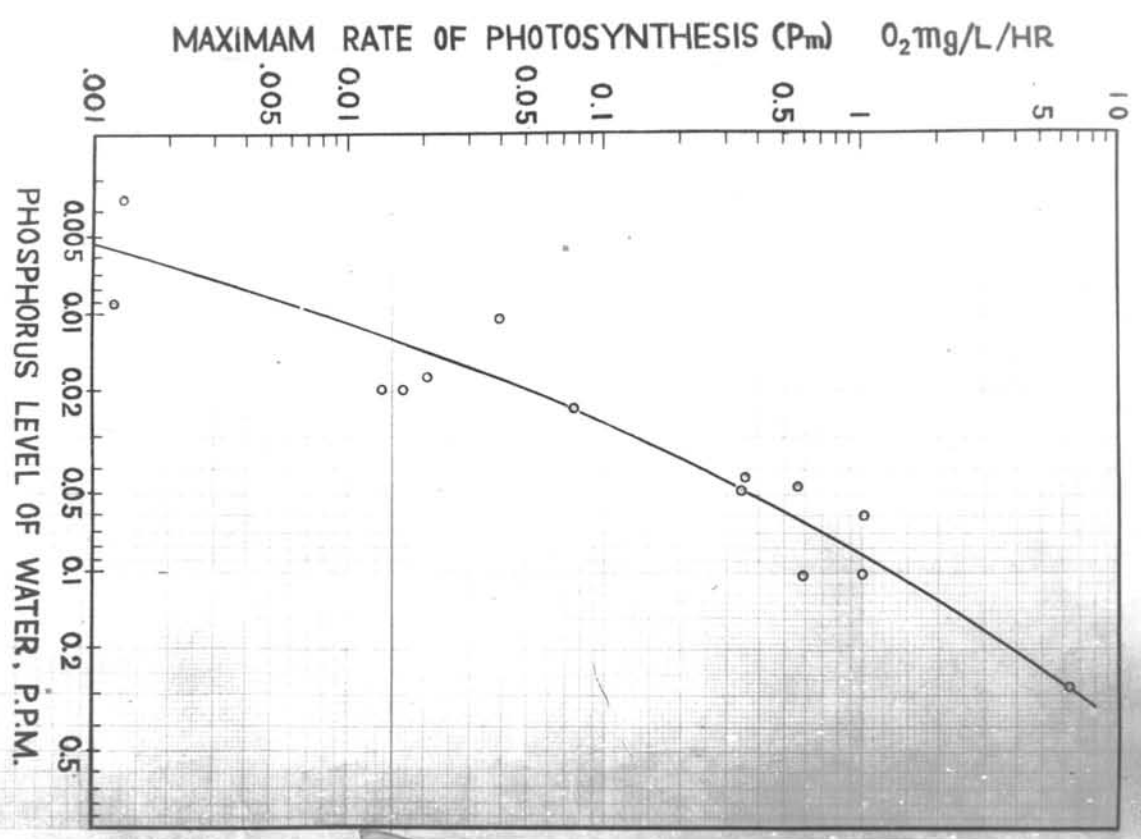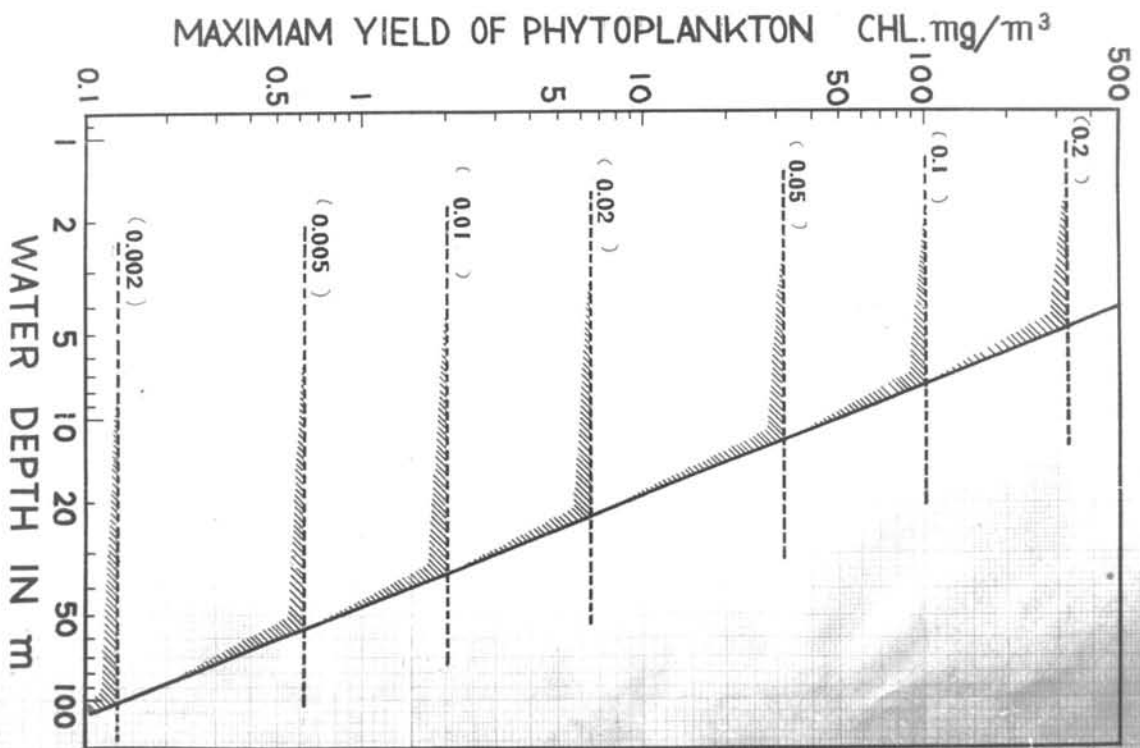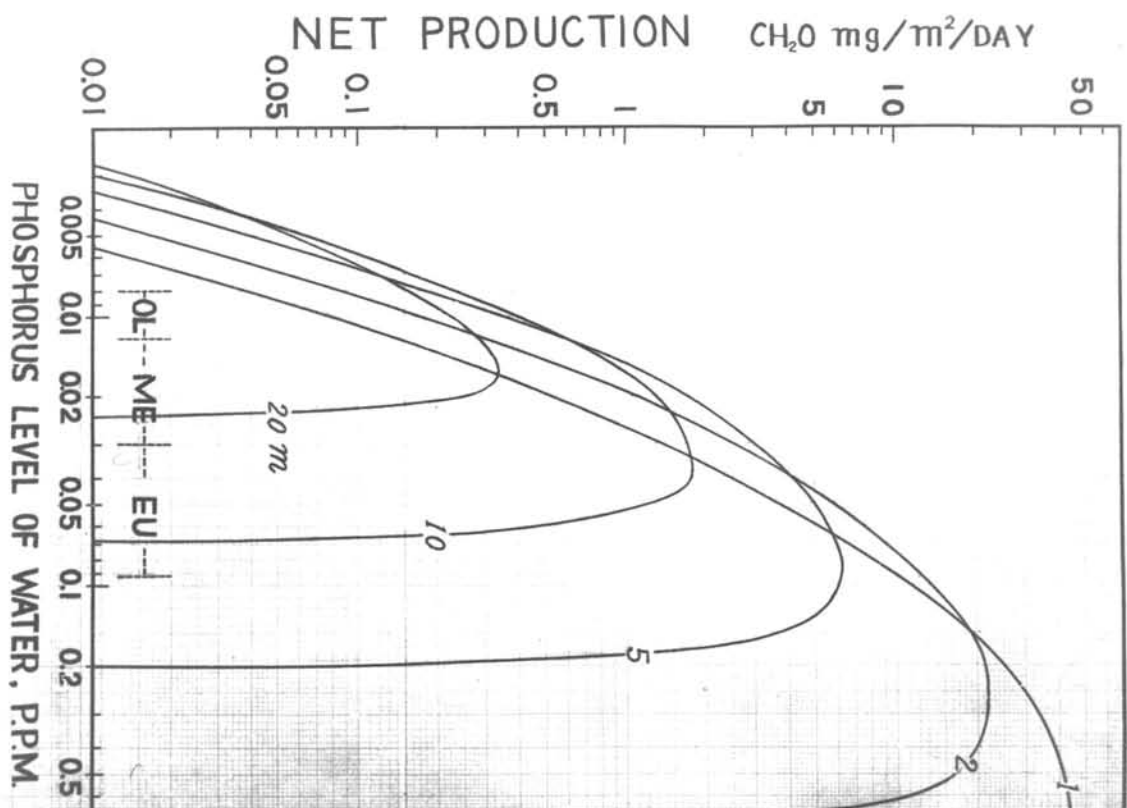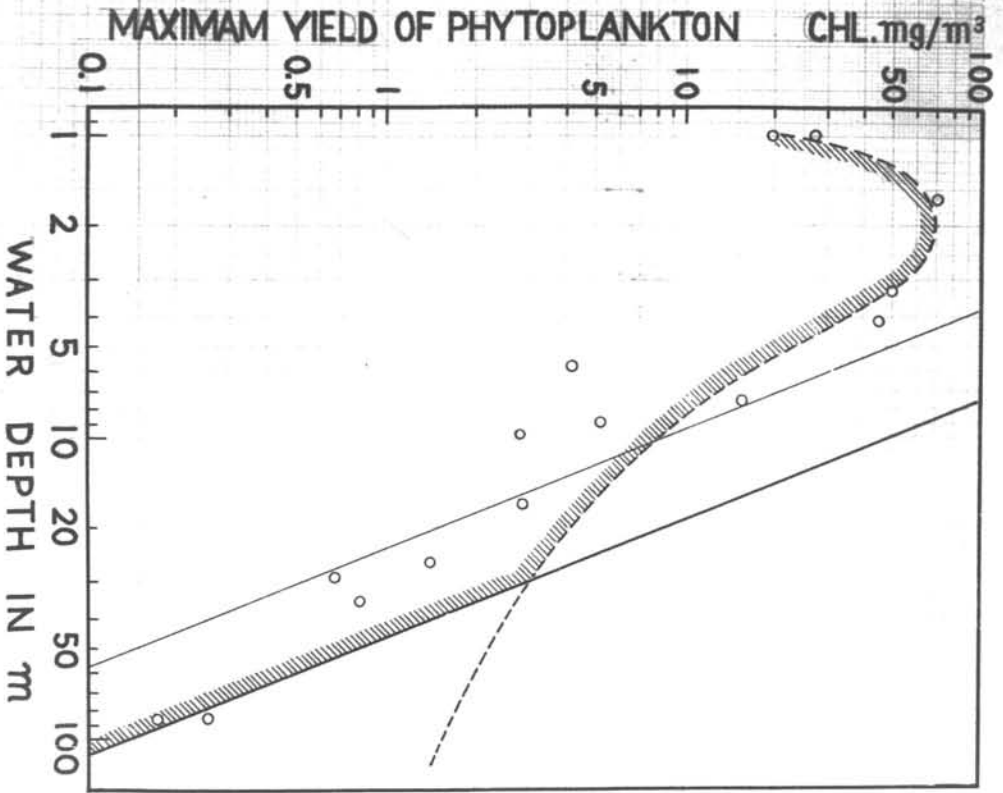
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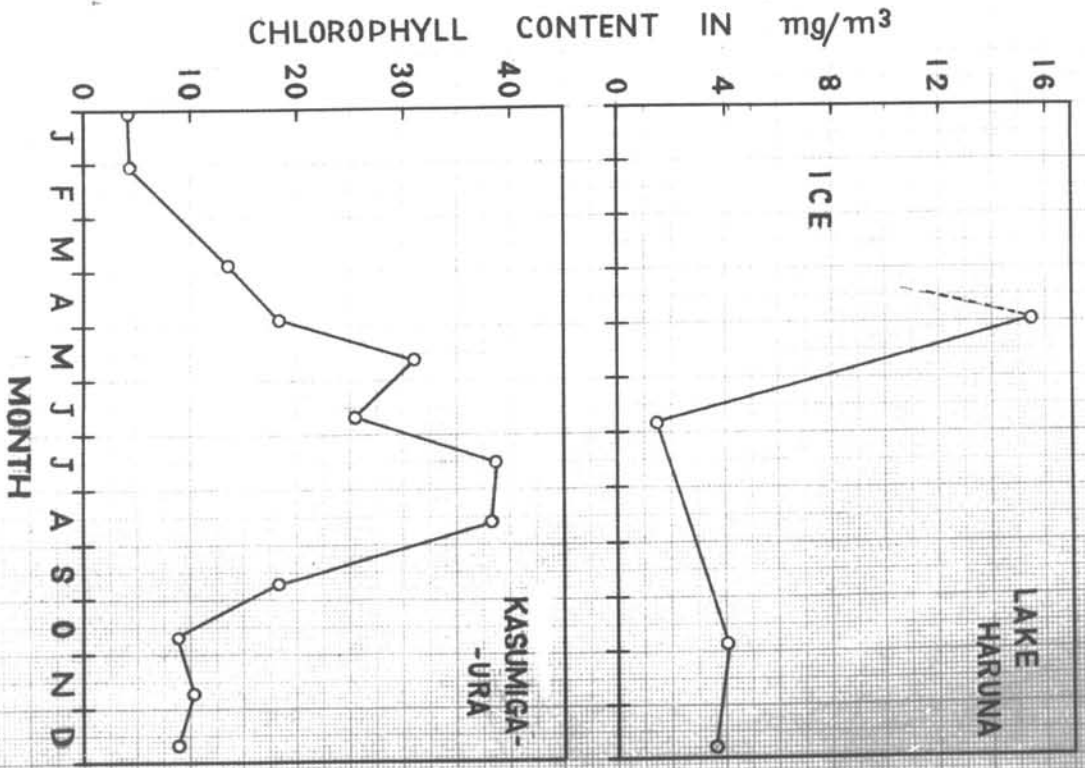
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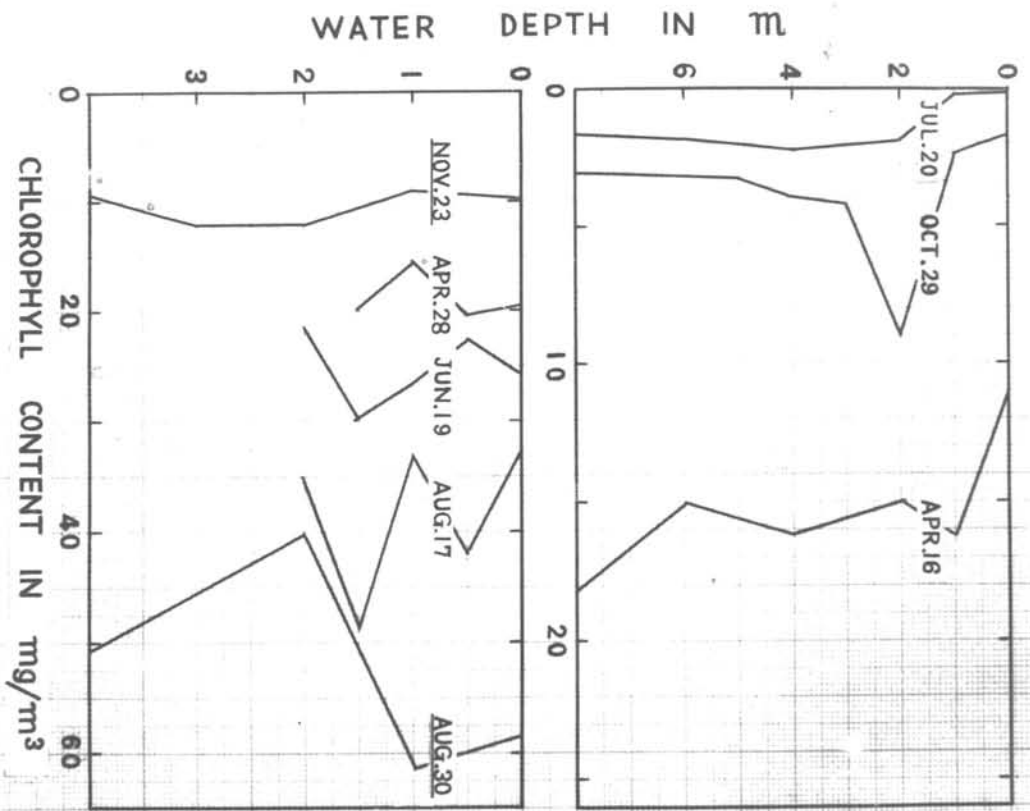
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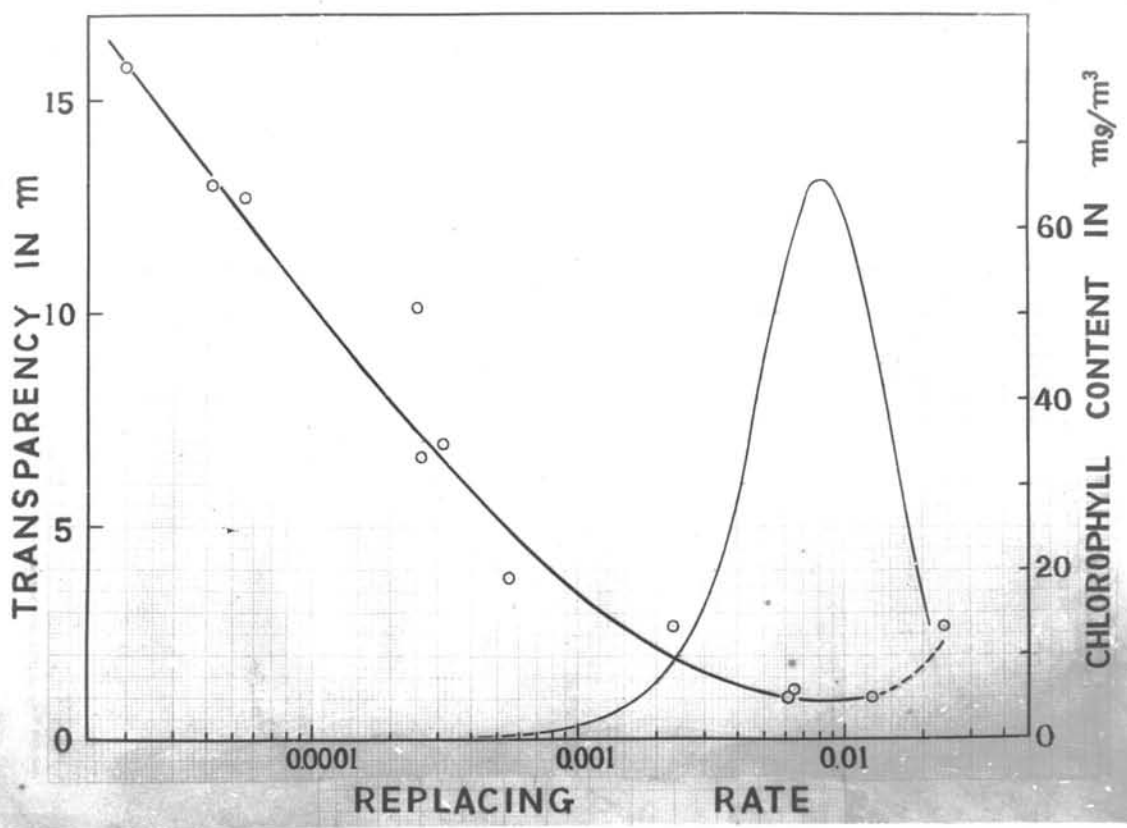
Fig. 21

Fig. 22
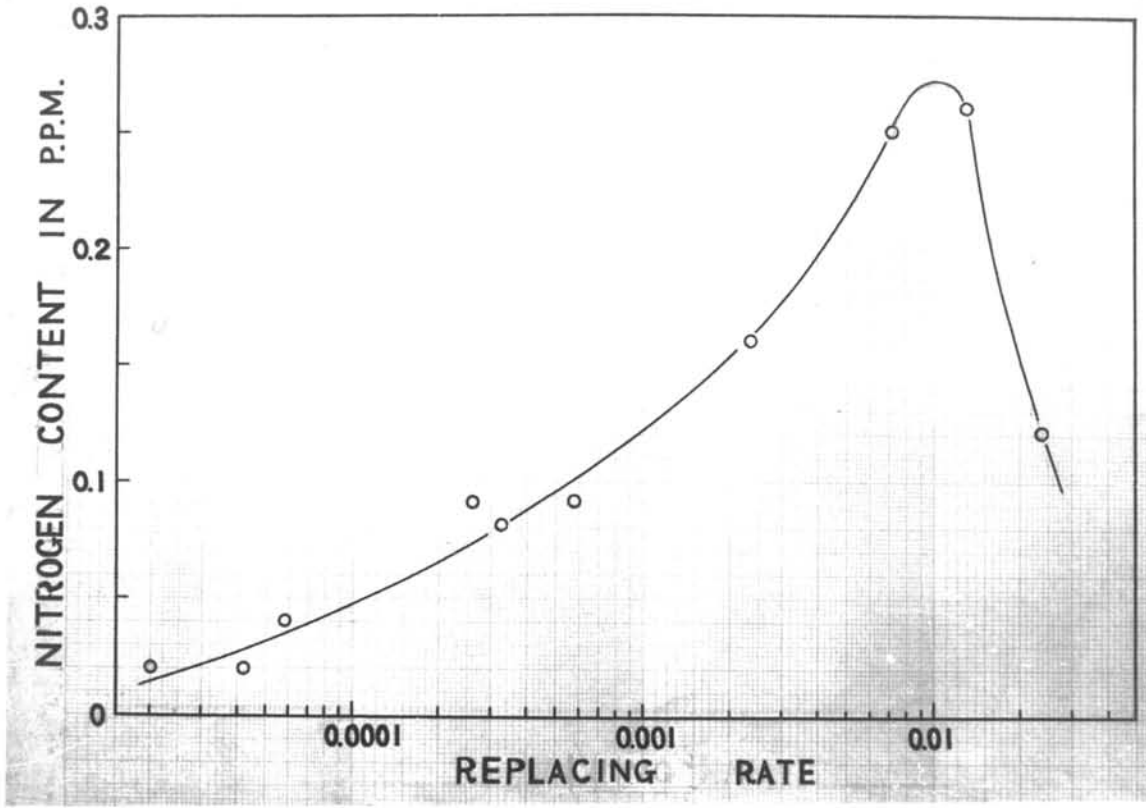
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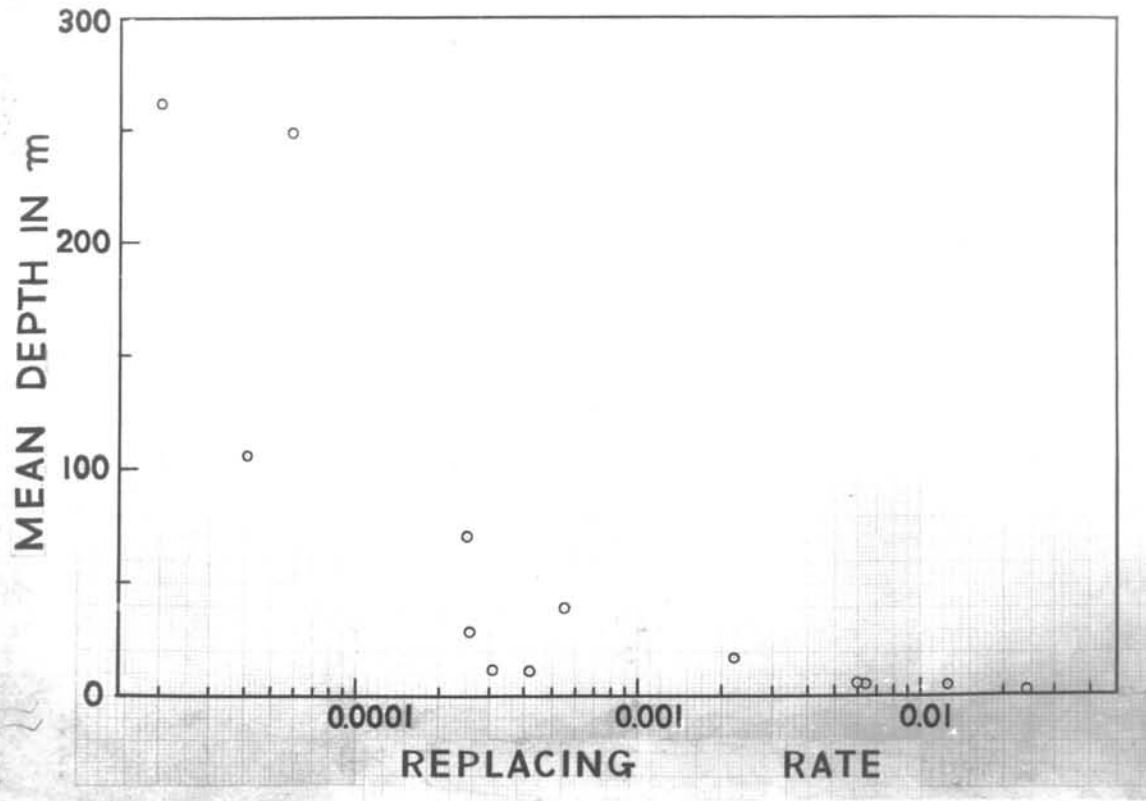
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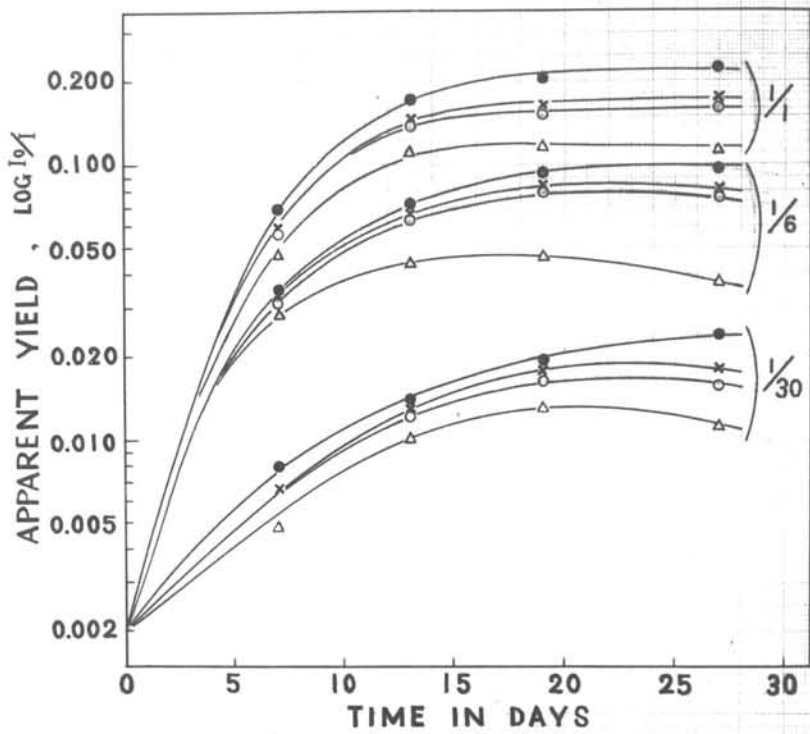
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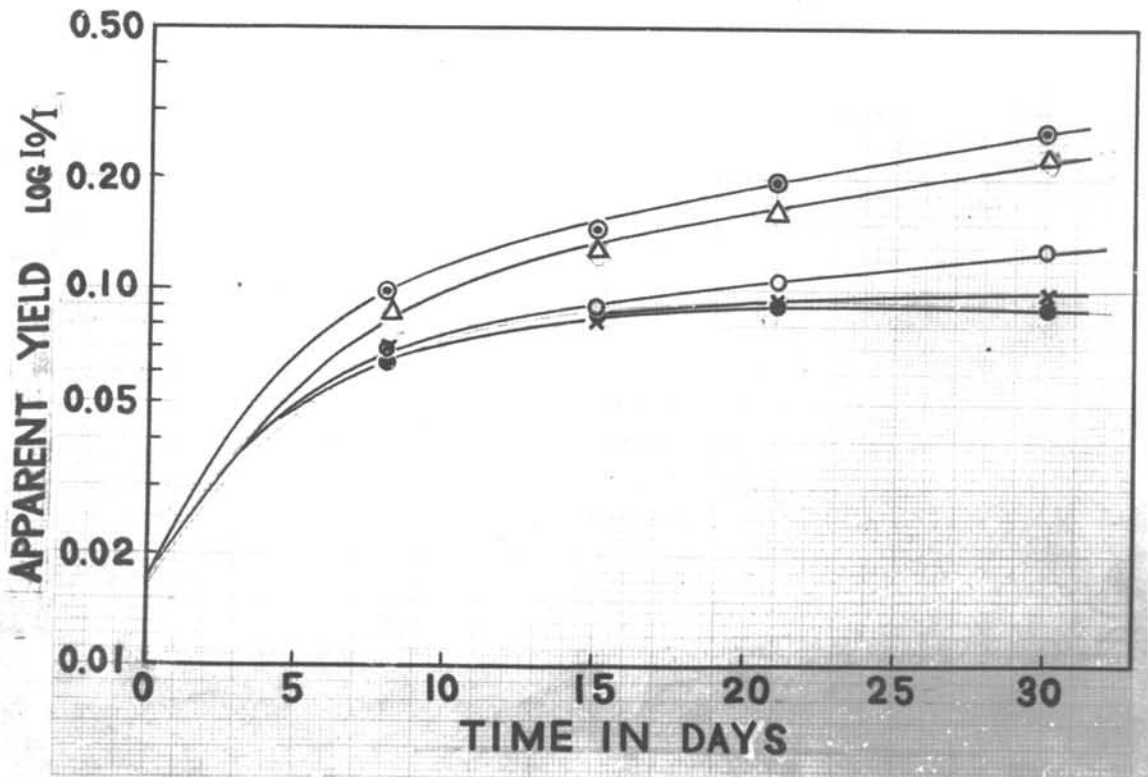
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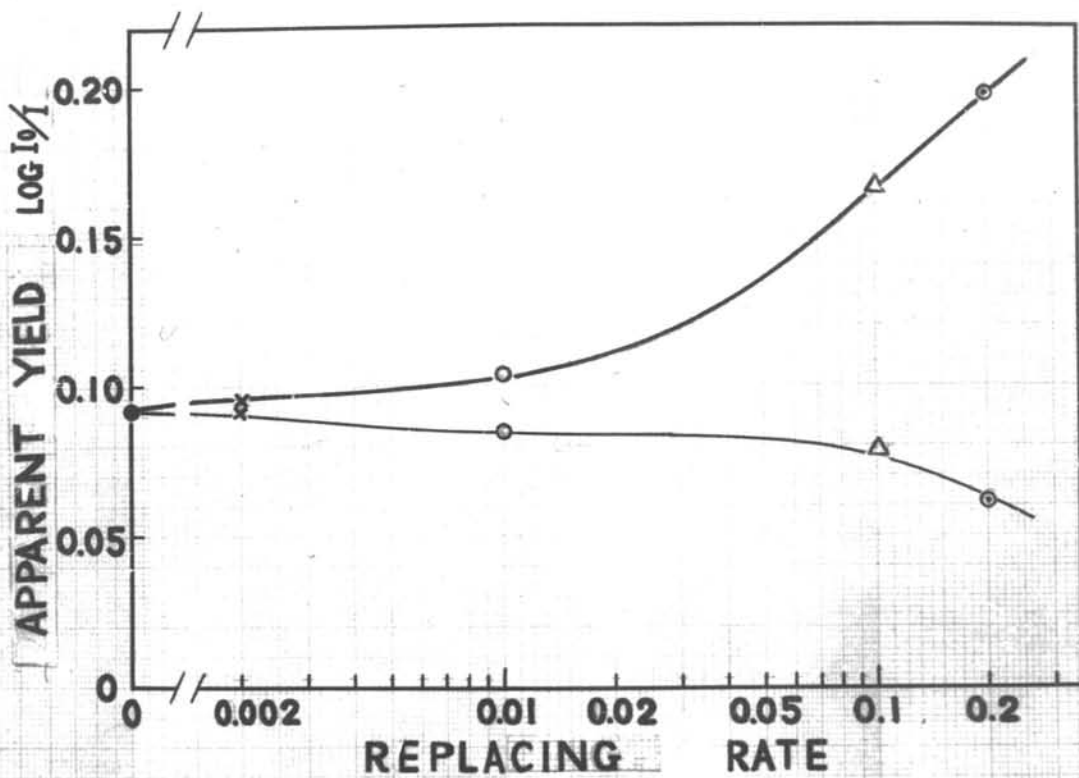
Fig. 27

Fig. 28

Fig. 29

Fig. 30

Fig. 31

THE AMOUNT OF SEDIMENT AFTER A YEAR , g/m^2

REPLACING RATE

Fig. 32

THE AMOUNT OF LIBERATED NUTRIENT SALTS
AFTER A YEAR , g/m^2

REPLACING RATE

Fig. 33