Ecological Studies on the Productivity of Aquatic Plant Communities III.

Effect of Depth on Daily Photosynthesis in Submerged Macrophytes

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Abstract

An attempt is made to calculate the absolute amount of daily photosynthesis in submerged plants at various depths and under different weather conditions on the basis of photosynthesis-light intensity curve and surface and subsurface light intensity records, with reference to transparency and light extinction coefficient of water. Theoretical daily gross photosynthesis-depth curves well correspond to the vertical distribution of daily photosynthesis in natural communities of submerged macrophyte and that of phytoplankton in stagnation period of lakes and ocean.

A logical interpretation is given to the empirically known correlation between compensation depth for aquatic green plants and transparency of water. Daily compensation depth for different seasons and weather conditions are in inverse proportion to the corresponding light extinction coefficient of water, or in proportion to the value of transparency. The monthly mean of daily compensation depth/transparency ratio for Elodea occidentalis in Lake Biwa is 2.0, 2.4 and 1.4 in January, April and July-August respectively. The ratio for Chlorella ellipsoidea ranges from 0.9 (rainy day, January) to 2.5 (fine day, July-August). It is noted that compensation depth is usually about twice as large as transparency. Considering that physiological activities of shoots, especially photosynthesis, are less active in basal parts of submerged macrophyte community than in upper parts, it is concluded that the daily compensation depth for the whole community might be considerably smaller than the values here calculated for apical parts of shoots.

A considerable amount of knowledge on the primary production of submerged plant communities has been accumulated since the attempt by Rickett to estimate the biomass of aquatic plants. Especially macrophyte communities in shallow waters studied by many investigators, whereas no satisfactory methods have yet been established for assessing the productivity of the communities in deep waters.

The method developed by Monsi and his coworkers, which intends to estimate the total matter production of a terrestrial plant community by combining the photosynthetic capacity of leaves with the light profile within the community, may also be suitably applied to submerged macrophyte and phytoplankton communities. In the present paper, an attempt is made to estimate the amount of daily photosynthetic production of submerged macrophyte communities according to their method, based

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on light-photosynthesis curve and surface and subsurface radiation data. Mathematical formulations are developed to calculate the daily production at different depths of water, at different degree of water turbidity, and under different conditions. Furthermore, a theoretical estimation of compensation depth is suggested with reference to the transparency of water.

Materials and Methods

Three species of submerged macrophytes, *Elodea occidentalis*, *Hydrilla verticillata* and *Vallisneria asiatica* var. *biwaensis*, were used as the material plants. The plants and the water used in the experiments were taken from 1.5-3 m depths of Lake Biwa in central Japan, the largest inland water of this country. Photosynthesis and respiration of the plants were measured at Miyagahama by the lake on April 16-17 and July 28-29 in 1964, and at Chiba on January 21 and 23 in 1965. The measurements were made in 2-hour periods from 11 a.m. to 1 p.m. on fine days by the light and dark bottle technique described in the preceding paper. In order to let the bottles receive several different levels of light intensity, they were kept at different depths in the lake in April and July, while they were placed in a large water tank covered by different numbers of sheets of cheese cloth in January. Both photosynthetic and respiration rate were expressed by mg oxygen evolved per g oven-dry weight of plant per hour.

Incident light intensity over the water surface, light extinction coefficient of the water and water temperature at each depth were simultaneously recorded every time. Continuous observations of total solar radiation and light intensity on a horizontal plane were also kept at the campus of the Chiba University using an Epply pyrheliometer, a Robitzsch actinometer and a selenium photocell.

Results

1. Photosynthetic rate and light intensity

The relation between light intensity and gross photosynthesis in apical portions of shoots taken from the surface of *Elodea occidentalis* community in January and April is given in Fig. 1. The light-saturated rate of photosynthesis nearly reached 7 mg O$_2$/g/hr. in both months, while the respiration rate was 0.5 and 0.8 mg O$_2$/g/hr. at water temperatures of 7° ± 1° and 10° ± 1° in January and April respectively.

Apical portions of shoots or leaves of *Elodea occidentalis*, *Hydrilla verticillata* and *Vallisneria asiatica* var. *biwaensis* exhibited nearly the same photosynthetic rate at light saturation and gave similar light-photosynthesis curves at 27° ± 2° of water temperature, so that the gross photosynthetic activity in the three species may reasonably be brought up together
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as shown in Fig. 2. A slight depression of photosynthesis was observed in all species under high light intensity or at about 80 klux. The respiration rate in July was 1.4, 1.9 and 1.3 mgO₂/g/hr. in E. occidentalis, H. verticillata and V. asiatica var. biwaensis.

Both light-saturated photosynthesis and respiration were more active in July than in January and April; consequently the value of compensation light intensity increased from about 0.2 klux in January and April to about 1 klux in July.

As already pointed out by many authors, a rectangular hyperbola given by the formula,

\[ p = \frac{bI}{1+al} \]

can well describe the relation between photosynthetic rate \( \, \text{mgO}_2/\text{g/hr.} \) and light intensity \( \text{klux} \) as shown by solid lines in Figs. 1 and 2. The constants \( a \) and \( b \) characterize the asymptote or the light-saturated rate of photosynthesis and the initial gradient of the curve at the origin.

2. Attenuation of light and transparency in the lake

Light intensity in water decreases exponentially with increasing depth, or the light intensity at \( z \) m depth is approximately given by the Beer-Lambert's law,

\[ I = I_0 \exp (-\lambda z) \]

where \( I_0 \) (klux) is the light intensity at a depth 0.01 m under the water surface, and \( \lambda(1/m) \) is the coefficient of light extinction in the water. Fig. 3 (right) illustrates the linear relationships between \( \log(I/I_0) \) and \( z \) expected from Eq. (2).

Another measure related to the extinction of light in waters is transparency (\( Tr \) m), which has long been used to indicate the turbidity of water or the thickness of trophogenic layer. Kikuchi proposed an empirical formula that represented the inverse proportionality between extinction coefficient and transparency,

\[ \lambda \cdot Tr = 1.9 \]

This was later confirmed by Ichimura based on the observations in several lakes of central Japan.

Comparable observations on the subsurface attenuation of light were made with
a selenium photocell and a Secchi disk around noon on fine days (August 19-21, 1965) at several different localities in Lake Biwa (Fig. 3, left). The range of depth covered was from 1.1 to 5.6 m. The results were also well approximated by Eqs. (2) and (3), which are to play important role in the following treatments.

3. Daily curve of light intensity

Daily courses of incident light intensity and total solar radiation on a horizontal plane were observed at Chiba (ca. 35 km southeast of Tokyo) in January, April and

Fig. 3. (Right) Relation between water depth and relative light intensity (in log scale) in Lake Biwa. A, Ogoto; B, Simo-Sakamoto; C, Minamihama; D, Katata; E, Okinosima.
(Left) Relation between transparency and light extinction coefficient in Lake Biwa. A smooth curve based on Eq. (3) well fits the experimental values.

Fig. 4. Diurnal curves of light intensity (L) and solar radiation (R) at the ground level at Chiba, on clear days in January (Left) and April (Right).
L: Thick broken lines, square sine curve (Left) and cubic sine curve (Right).
R: Fine broken lines, sine curves.
August in 1964 and 1965. As illustrated in Fig. 4, the light intensity \( I \) (klux) at a given time \( t \) hours from sunrise on clear days can fairly well be described by the following equations.

\[
I = I_{\text{max}} \sin^2 \omega t \quad \ldots\ldots (4)
\]

and

\[
I = I_{\text{max}} \sin^3 \omega t \quad \ldots\ldots (5)
\]

In these equations, \( I \) attains its maximum value \( I_{\text{max}} \) (klux) at the highest altitude of the sun, and the constant \( \omega \) is determined by the measurement of the day-length.

The day-length is given as \( \pi/\omega \) (hour). \( I_{\text{max}} \) and \( \omega \) may vary according to latitude, season and weather condition. Eq. (5) fits very well to the light intensity curve on clear days from spring to fall, whereas Eq. (4) is better applicable to the curves on clear days in winter and on cloudy and rainy days in the four seasons (Figs. 4 and 5). The constant \( I_{\text{max}} \) on a clear day and \( \omega \) in the three seasons concerned at Chiba are as follows:

<table>
<thead>
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<tbody>
<tr>
<td>( I_{\text{max}} ) (klux)</td>
<td>40</td>
<td>100</td>
</tr>
<tr>
<td>( \omega ) (1/hr.)</td>
<td>( \pi/10 )</td>
<td>( \pi/13 )</td>
</tr>
</tbody>
</table>

Daily marches of light intensity under fine, cloudy and rainy sky in July observed at Toride (ca. 30 km northeast of Tokyo) by Iwaki and Nomoto\(^9\) are illustrated in Fig. 5. Relative value of daily maximum light intensity \( (I_{\text{max}}) \) were 100, 56 and 22\% on clear, cloudy and rainy days in this case. In order to avoid too much complexity in the following calculations, the relative values of daily light maxima corresponding to the three weather conditions were assumed to be 100 (clear and half-cloudy), 50 (cloudy) and 25 (rainy). Similar relationships have already been demonstrated by Ikusima\(^{10}\) with respect to total solar radiation.

Mathematical Representation of Daily Photosynthesis

Gross photosynthesis of a given part of a submerged plant depends upon such environmental factors as incident light intensity, light attenuation in water, water temperature, and concentrations of carbon dioxide, oxygen and other dissolved nutrients as well as upon internal physiological factors. In the following, only the light factor which is directly affected by water depth is considered as the first approximation.

From Eqs. (1), (2) and (4) or (5), the mean hourly rate of gross photosynthesis at time \( t \) and depth \( z \) \( (p(t, z) \text{ mgO}_2/\text{g/hr.}) \) is expressed by the following equations.

\[
p_2(t, z) = \frac{bI_{\text{max}} \exp (-\lambda z) \sin^2 \omega t}{1 + aI_{\text{max}} \exp (-\lambda z) \sin^2 \omega t} \quad \ldots\ldots (6)
\]

and

\[
p_3(t, z) = \frac{bI_{\text{max}} \exp (-\lambda z) \sin^3 \omega t}{1 + aI_{\text{max}} \exp (-\lambda z) \sin^3 \omega t} \quad \ldots\ldots (7)
\]
where Eq. (6) gives the mean hourly rate of gross photosynthesis on clear days in winter and on cloudy and rainy days in the four seasons, and Eq. (7) fits to that on clear days from spring to fall. The daily gross photosynthesis \( q(z) \text{ mgO}_2/g/day \) can then be obtained by integrating \( p(t, z) \) over the entire daylength as follows,

\[
q_2(z) = 2 \int_0^{\pi} p_2(t, z) dt = C(1 - B), \quad \cdots \quad (8)
\]
as it is difficult to calculate \( q_3(z) \) from \( p_3(t, z) \), and the method of calculating from \( p_2(t, z) \) and \( p_4(t, z) \) is used here.

\[
q_3(z) = 2 \int_0^{\pi} p_3(t, z) dt = \frac{1}{2} \left\{ 2 \int_0^{\pi} p_2(t, z) dt + 2 \int_0^{\pi} p_4(t, z) dt \right\} = \frac{C}{2} \left[ 2 - B - \left\{ \left( B + B^3 \right)/2 \right\}^{1/2} \right] \quad \cdots \quad (9)
\]

where

\[
B = \left\{ 1 + aI_{\text{max}} \exp \left( -\lambda z \right) \right\}^{-1/2},
\]

\[
C = \frac{\pi b}{\omega a},
\]

and

\[
p_4(t, z) = \frac{bI_{\text{max}} \exp \left( -\lambda z \right) \sin^4 \omega t}{1 + aI_{\text{max}} \exp \left( -\lambda z \right) \sin^4 \omega t}.
\]

Eqs. (8) and (9) represent the daily gross photosynthesis-depth curve with the light extinction coefficient \( \lambda \) as a parameter. It is worth of note that \( q(z) \) is proportional to \( \pi/\omega \) or length of daytime. As stated before, Eq. (8) should be applied to clear days in winter and cloudy or rainy days in all seasons, and Eq. (9) to clear day from spring to fall.

The daily gross photosynthesis at the water surface is given by putting \( z = 0 \) in Eq. (8) as follows.

\[
q_2(0) = C \left\{ 1 - (1 + aI_{\text{max}})^{-1/2} \right\} \quad \cdots \quad (11)
\]

Eq. (11) is to correspond with the daily light-photosynthesis curve in leaves of terrestrial plants, and give the curve shown in Fig. 6. It is very similar in its trend with the conventional equation of rectangular hyperbola (Eq. (1)) widely applied to various terrestrial plants including grasses, herbs and trees\(^6\,^8\,^{11}\).

Daily gross photosynthesis-depth curves for different weather conditions were calculated in this way and illustrated in Fig. 7 with \( \lambda \) as the parameter. It seems

Fig. 6. Relative light intensity-daily gross photosynthesis curves in *Elodea occidentalis* in July–August. Solid and broken lines are respectively based on Eqs. (11) and (1).
Fig. 7. Changes of daily gross photosynthesis with water depth, based on theoretical Eqs. (8) and (9). $a=0.189$, $b=1.72$, $\omega=\pi/13.5$ and $I_{\text{max}}=122$ (fine), 61 (cloudy), and 30.5 (rainy). Dotted lines represent daily respiration ($r$). A; Elodea occidentalis, $r=33.6$, B; Hydrilla verticillata, $r=45.6$. From left to right: fine day, cloudy day and rainy day in July-August.

Fig. 8. Vertical distributions of the monthly means of daily gross photosynthesis of Elodea occidentalis in Lake Biwa, calculated from Eqs. (8) and (9). Dotted lines represent daily respiration. From left to right: January, April and July-August. The constants are as follows: January; $a=0.872$, $b=6.46$, $r=12.0$, $\omega=\pi/10$ and $I_{\text{max}}=40$ (fine day), April; $a=0.872$, $b=6.46$, $r=19.2$, $\omega=\pi/13$ and $I_{\text{max}}=100$ (fine day), July-August; All constants are the same as in Fig. 7.
from the result of preliminary surveys that the range of $\lambda$ from 0.3 to 1.5 (1/m) or that transparency from 6.3 to 1.3 m is most commonly encountered in lakes and still waters where submerged macrophytes grow luxuriantly. Different values of $\lambda$ resulted in different trends of the curve, more rapid decline of daily photosynthesis with increasing water depth being associated with greater value of $\lambda$. Apparently these curves well agree in general trends with the daily photosynthesis-depth curves experimentally obtained in a well-developed Vallisneria denserullata community$^{10}$, and in natural phytoplankton communities of lakes$^{12}$ and ocean$^{13}$. It became evident from Fig. 7 that the amount of daily photosynthesis at the upper parts of water column on a cloudy day is comparable with that on a clear day, in spite of the reduction of $I_{max}$ by half.

Monthly means of daily photosynthesis of Elodea occidentalis in Lake Biwa were also calculated for the three months based on the average frequency record of each weather type at Hikone on the eastern shore of the lake$^{14}$. The average frequencies of the three weather types are 33 (clear and half-cloudy) : 43 (cloudy) : 24 (rainy and snowy), 46 : 37 : 17 and 45 : 45 : 10 in January, April and July-August respectively. As Fig. 8 shows, high photosynthetic activity is maintained from spring to summer. Considering the presence of other species, the highest production by submerged macrophytes in Lake Biwa seems to occur in early summer.

**Daily Compensation Depth as a Function of Light Attenuation in Water**

Under natural conditions, the compensation depth for an aquatic plant may vary from hour to hour with ever-changing light intensity, even if the light-compensation point remains constant. To have an exact understanding of the lower limitation of the vertical distribution and the matter production of aquatic communities, the compensation depth should therefore be considered on a daily basis or on a monthly mean basis.

Daily compensation depth may be graphically determined in Figs. 7 and 8 as the abscissa of the point where the depth-curves for daily photosynthesis and daily respiration intersect. Since the respiration rate obtained by in situ method in spring and summer remained more or less constant irrespective of depth, the effect of temperature on respiration may be disregarded at least within the range of a few degrees. Daily respiration was thus estimated as the mean hourly respiration rate times 24 hours. Figs. 7 and 8 show that the daily compensation depth differs according to the change of $\lambda$ or $T_{y}$.

Daily compensation depth ($z_{c}$ m) can also be obtained by combining daily respiration rate ($r$ mgO$_2$/g/day) with Eq. (8) or with Eq. (9), viz.

\[ q_{2}(z_{c}) = r, \]

and

\[ q_{3}(z_{c}) = r. \]

From Eqs. (8), (10) and (12), $z_{c}$ is calculated as follows.

\[ z_{c} = -\frac{1}{\lambda} \ln \frac{1}{a I_{max}} \left\{ \left( \frac{C}{C-r} \right)^{2} - 1 \right\} \]

Putting

\[ -\ln \frac{1}{a I_{max}} \left\{ \left( \frac{C}{C-r} \right)^{2} - 1 \right\} = K(\text{const.}), \]

we have

\[ z_{c} = \frac{K}{\lambda}. \]
Combining Eq. (16) with Eq. (3), it is expected that

\[ z = K \frac{m}{r}. \]  

The final formula, Eq. (17), gives a theoretical interpretation to the empirically known fact that the compensation depth for aquatic green plants can be expressed as a linear function of transparency. It must be noted here that the constant \( K \) in Eq. (17) is expressed in terms of certain physiological properties of the plant such as the photosynthetic capacity given by \( a \) and \( b \) and the respiration rate \( r \) as well as of such environmental parameters as \( I_{max} \) and \( \omega \) (Eq. 15).

The values of \( z \) of Eq. (13) graphically estimated from Figs. 7 and 8 were also proved to be in inverse proportion to \( \lambda \) or to be proportional to \( Tr \).

It has already been reported by some authors\((8,15,16)\) that the experimentally determined values of the ratio, daily compensation depth(m)/transparency(m) or \( z/Tr \), were nearly equal to 2 in certain lakes of different trophic levels. Calculated values of the ratio for Elodea occidentalis and Hydrilla verticillata are given in Table 1. The ratio depends on relative intensity of \( I_{max} \) as well as on weather conditions as shown in Fig. 9. On a monthly mean basis, \( z/Tr \) for \( E. occidentalis \) was 2.0, 2.4 and 1.4 in January, April and July-August.

In Table 2 is presented the \( z/Tr \) ratio calculated by means of Eq. (17) for the green algae, Chlorella ellipsoidea, studied by Aruga\((17)\). The ratio seems almost independent of the temperature change between 10° and 30°, ranging from 0.9 on a rainy day in January to 2.5 on a fine day in

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**Table 1.** Daily compensation depth(m)/transparency(m) or \( z/Tr \) for Elodea occidentalis and Hydrilla verticillata under different weather conditions in July-August.

<table>
<thead>
<tr>
<th>Condition</th>
<th>( E. occidentalis )</th>
<th>( H. verticillata )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fine and half-cloudy</td>
<td>1.6</td>
<td>1.3</td>
</tr>
<tr>
<td>Cloudy</td>
<td>1.4</td>
<td>1.1</td>
</tr>
<tr>
<td>Rainy</td>
<td>1.0</td>
<td>0.7</td>
</tr>
</tbody>
</table>

**Table 2.** The ratio \( z/Tr \) in Chlorella ellipsoidea under different weather conditions calculated by Eq. (17) from the data obtained by Aruga\((17)\).

<table>
<thead>
<tr>
<th>Condition</th>
<th>January</th>
<th>April</th>
<th>July-August</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fine and half-cloudy</td>
<td>1.7</td>
<td>2.4</td>
<td>2.5</td>
</tr>
<tr>
<td>Cloudy</td>
<td>1.3</td>
<td>2.0</td>
<td>2.1</td>
</tr>
<tr>
<td>Rainy</td>
<td>0.9</td>
<td>1.6</td>
<td>1.8</td>
</tr>
</tbody>
</table>
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July–August. These theoretical values agree fairly well with the experimental values obtained by other investigators\(^8,10\).

As for the basal portions of shoots of *E. occidentalis*, daily gross photosynthesis- and daily respiration-depth curves assume the trends illustrated in Fig. 10. Both photosynthesis and respiration were less active in basal parts of shoot than in apical parts. The deterioration of photosynthetic activity was especially remarkable in bleached shoots at the bottom of the community\(^6,10\). The daily gross photosynthesis in such portions of shoot could not compensate the daily loss of matter by respiration even at the water surface except on a clear day. Interception of light by apical parts of shoot is another factor that influences the matter budget in basal parts. The relative light intensity within the community about 1 m below the community surface was only about 1/20 of the intensity at the surface. Lower layers of the community which possessed nearly one half of the total biomass of photosynthetic organs, therefore, contributed negatively to the total matter budget of the whole community, especially in foul weather. It may thus be concluded that the actual daily compensation depth for the whole community is considerably smaller than the values given in Figs. 6 and 7 and Table 1.

The author wishes to thank Prof. Makoto Numata of the Chiba University and Prof. Tatuo Kira of the Osaka City University for their helpful suggestions and criticisms. Thanks are given to Mr. Hajime Kabaya and Miss Yōko Watanabe for their assistance in the experimental work. The research was supported in part by Grant in Aid of Scientific Research of the Ministries of Education and Construction.

References

12) Ichimura, S., ibid. 69 : 7 (1956).  
生崎 功： 水生植物群落の生産力についての生態学的研究 III．
沈水大型植物の日光合成量における水深の影響

光合成—光曲線と水面または水中における光の弱さの日変化を組みあわせて、任意の水深にある水中の緑色植物の 1 日の光合成を天気や潮の透明度または吸光係数を考慮してもとめた。

日総光合成量—水深の関係を生理的要因（光合成や呼吸の能力）と環境要因（日最大水平照度、日照時数や水中照度）の関数として (8), (9) 式でしめた。この式がしめす理論曲線は自然でみられる沈水大型植物や湖沼・海洋の停滯期にみられる植物プランクトンの 1 日の光合成量の垂直分布によくあった。

水中の緑色植物の補償深度は、それらが生育している水体の透明度をよく対応するというこれまでの経験的な法则に対して、理論的な根拠をもたえた。春から秋にかけての晴天下では日補償深度はグラフから（図 7, 8）、冬の晴天および四季をつうしての陰天・雨天での日補償深度は（16）、（17）式から理論的にもとまる。このようにしてともえた日補償深度は吸光係数に反比例し、透明度に比例する。

琵琶湖に生育する Elodea occidentalis について月平均の補償深度/透明度の値（上の関係における比例定数）をもとめたと 1 月は 2.0, 4 月は 2.4, 7～8 月は 1.4 となった。Chlorella ellipsoidea についての補償深度/透明度の値は、1 月の雨天の 0.9 から 7～8 月の晴天における 2.5 の範囲にあった。補償深度が透明度のほぼ 2 倍の深さに一致することは注目される。

群落下層部の葉茎の日総光合成量や日呼吸量は群落上層部の葉茎のそれよりも小さい値であり、とりわけ光合成能の低下は著しい。このことからも群落全体についての日補償深度は、単に群落上層部の葉茎のみから算出した深度よりさらに浅い位置にあると考えてよい。（千葉大学文理学部生物学教室）