The Chlorophyll "A" of Communities

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Introduction

Spreading over the earth in vast variety are endless ecosystems making ecological magic from sunbeams. When viewed from far above, some of the differences among systems are not visible and there is only one dark green carpet. In the uniformity of

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greenness, therefore, one may search for some generalization in life's diversity. In this paper the ecological role of green chlorophyll is considered, and a role of chlorophyll in regulating input-output energetics is postulated. It is suggested that ecological requirements are a dominant factor in evolutionary and successional fabrication of systems controlling chlorophyll chemistry in nature.

It is presumed that machinery for purposeful adjustment of chlorophyll for the best use of light by the natural community was established through natural selection. Non-mechanistic teleology is nowhere implied.

In 1918 Willstatter and Stoll summarized the results of their studies relating photosynthesis and chlorophyll. They reasoned that photosynthesis might be proportional to the amount of chlorophyll and introduced the concept of the assimilation number, which was defined as the ratio of photosynthetic rate to the weight of chlorophyll. Although similar assimilation numbers were found by early workers among many different land plant species, differences were shown related to age, light, nutrition, and other factors. There is now an important full science of the physiology of chlorophyll in plant tissues and cells (Rabinowitch, 1945, 1951, 1956).

The attempts to use chlorophyll as a measure of the overall photosynthetic function in ecological systems began with Harvey (1934), who used visual estimates of green pigments extracted from marine planktonic communities as an estimate of the phytoplankton biomass. Following these early beginnings chlorophyll, especially chlorophyll "A", has been widely measured to characterize communities of aquatic plankton. At present a considerable literature describes quantitatively the chlorophyll in communities and cultures under many circumstances. Chlorophyll was not found to be a perfect measure of biomass of plants, but many authors have related the amount of photosynthesis to the amount of chlorophyll as Willstatter and Stoll had done (Manning and Juday, 1941; Riley, 1940; Ryther and Yentsch, 1957). Unfortunately a large range in assimilation numbers was found among different populations and conditions. Thus the use of chlorophyll as an indicator of photosynthesis has been demonstrated only in situations where the quantitative behavior of the assimilation number has been known. As used here, chlorophyll "A" is an extractable pigment fraction defined spectrophotometrically. It is recognized that more than one chemical entity may be involved.

Because chlorophyll is involved in the initial events of photosynthesis, assimilation is related to the first events of gross photosynthesis rather than to the net photosynthesis after the plant respiration has dispersed part of the energy. Little correlation was found between chlorophyll and net photosynthesis with the C^{14} method in the North Atlantic by Ketchum, Ryther, and Yentsch (Ryther and Yentsch, 1958). One can recognize the necessity for basing assimilation number on gross photosynthesis, a priori, by considering the case of a plant whose respiration balances its gross photosynthesis. There is assimilation and thus there should be an assimilation number value even though there is no net production. Rodhe, Vollenweider, and Nauwerck (1958) in lakes found that photosynthesis with the radiocarbon method was closely correlated with chlorophyll during the spring bloom period but did not correlate well in summer period. If as Ryther and associates have shown, radio-carbon methods yield net plant production, then no correlation would be expected except in the spring periods when net production and gross production are almost similar. All data and discussions here concern gross photosynthesis.

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Assimilation number as used in this paper is the ratio of grams oxygen produced per hour per gram of chlorophyll "A" in any situation whether under conditions of maximum assimilation or not. As evidenced elsewhere in this paper, whole communities rarely have a light saturation level so that the natural photosynthesis and maximum photosynthesis are the same.

Unfortunately measurements of gross photosynthesis require correction for the respiration during the illumination period. The night respiration rate is usually used for the correction on the assumption that night respiration and day respiration are similar. It is understood that respiration is probably not constant (Rabinowitch, 1956: 1925), but no easy way of determining day respiration in nature is as yet available. Thus uncertainties in the assumptions underlying the use of chlorophyll are likely to be as great as present uncertainties in the chemical determinations of chlorophyll.

In the following sections measurements are presented for natural communities of contrasting types in order to extend knowledge of the chlorophyll concentration and assimilation numbers of whole communities. First some aspects of chlorophyll extraction as used for field purposes in ecology are discussed. The cannon-ball catcher analogy is introduced to permit conceptual and hypothetical generalization concerning energy adjustment. Some reasons are given for expecting total community chlorophyll to be related to gross photosynthesis whereas mere parts of the euphotic zone may not be correlated. Then data from many sources on the distribution and variation of chlorophyll are reviewed. Finally, chlorophyll data from contrasting communities are presented on an area basis with suggestions for the use of assimilation numbers to compute photosynthesis.

Acknowledgement

These studies were aided by the National Science Foundation with Grant NSF G3978 on Ecological Microcosms. Studies in Puerto Rico were aided by the Rockefeller Foundation. We are grateful to Dr. Juan Rivero, Institute of Marine Biology, Mayaguez, Puerto Rico for providing facilities for studies in Puerto Rico and to Dr. Clarence Ayers and to Dr. Saul Kit for use of recording spectrophotometric equipment.

Chlorophyll Methods for Ecological Purposes

Analytical determinations of chlorophyll pigments have been widely accomplished spectrophotometrically. Several authors have calibrated such determinations to permit easy analysis for chlorophyll without chlorophyll standards being available. The procedure of Richards with Thompson (1952) and Creitz and Richards (1955) has been much used by ecologists. Other spectrophotometric computations are given by Mackinney (1941).

In Richards and Thompson's procedure after samples are extracted in 90 per cent acetone, optical densities (d) are measured in a 1 cm. optical path in square cuvettes at three wave lengths (630, 645, and 665 millimicrons). Then the chlorophyll "A" is computed with the relationship in equation (1) below. The measurement at 630 millimicrons was made to eliminate effects of pigments other than chlorophyll a and b. Duxbury and Yentsch (1956) provided a nomogram for rapid computations.

$$\text{Chlorophyll “A” in mg./L.} = 16.6\ d_{665} - 2.0\ d_{645} - 0.8\ d_{630} \qquad (1)$$

HORIZONTAL HETEROGENEITY

Aside from uncertainties in the procedure as described above, a number of additional sources of variation and error are involved in analyses of chlorophyll of diverse communities in nature. The difficulties of sampling from heterogeneous distributions are the most serious. For example replicate samples of adjacent bottom ooze in Laguna Madre of Texas contained 0.035, 0.078, 0.013, 0.022, 0.030, 0.021, 0.036, 0.024, 0.016, 0.018 gm./M^2 on Dec. 3, 1957; 0.081, 0.067, and 0.065 gm./M^2 on Feb. 15, 1958; and on Jan. 31, 1958, 0.270, 0.191, and 0.50 gm./M^2. Duplicate *Diplanthera wrightii* quadrat samples on Nov. 4, 1957 contained 0.163, 0.081, 0.061, and 0.027 gm./M^2 and 0.024, 0.028, 0.020, 0.020, 0.020, 0.018, and 0.022 gm./M^2 on Dec. 27, 1957. Duplicate quadrat samples of Thalassia from Redfish Bay, Port Aransas, Texas contained 0.480, 0.487, 0.190, 0.107 gm./M^2.

In addition there are difficulties with dead chlorophyll, solvents, portable spectrophotometer approximations, and varying pigment composition. In order to adapt the Richards and Thompson method to routine use in the field, several technique tests were carried out as summarized in the following paragraphs.

NON-FUNCTIONAL CHLOROPHYLL

If chlorophyll of natural ecosystems is to be related to gross photosynthesis, either the non-functional chlorophyll must be eliminated from the analytical determination, or some convention must be established as to its inclusion. The presence of non-functional chlorophyll has been reported frequently in the euphotic zone (Edmondson and Edmondson, 1947; Gillbricht, 1951; Krey, 1952).

It had been suggested by Ryther and Yentsch (1957) that careful narrow band spectrophotometry could be used to eliminate active Chlorophyll "A" from non functional chlorophyll. It was reasoned that chlorophyll "A" rapidly changed to phaeophytin or other compounds with a shift in the peak of its absorption spectrum away from 665 millimicrons.

In Figure 1 are presented absorption spectra of extracts in 90 per cent acetone with fresh material and materials experimentally aged and known to be non-functional. A spectrum from marine sediments in chloroform is also included from Orr and Grady (1955). Chloroform and acetone are 3 millimicrons apart in the positions for 665 peak of chlorophyll "A" (Rabinowitch, 1951: 640). From the similarity of peaks in Figure 1 it appears that chlorophyll of living and non-living materials in nature does not necessarily differ in spectral characteristics. Certainly if non-functional and live chlorophyll cannot be separated spectrophotometrically with a narrow band pass instrument, there is no possibility of eliminating the dead chlorophyll with a broad band pass instrument suitable for portable field use.

Instead of attempting to eliminate the non-functional chlorophyll it is suggested that the convention be adopted to include all chlorophyll "A" and related substances that affect the 665 millimicron spectrum if they occur within the euphotic zone. This convention has been used in this communication. The euphotic zone is defined as the zone between the top of the plants down to the level at which visible light is extinguished to about 1 per cent of full daylight. Both on land and in water the 1 per cent level may be readily located with a photometer. On land some leaf litter may be included. It seems likely that the variation in the per cent of non-functional chlorophyll in the euphotic zone may not be as great an error as that from heterogeneous distributions and sampling.

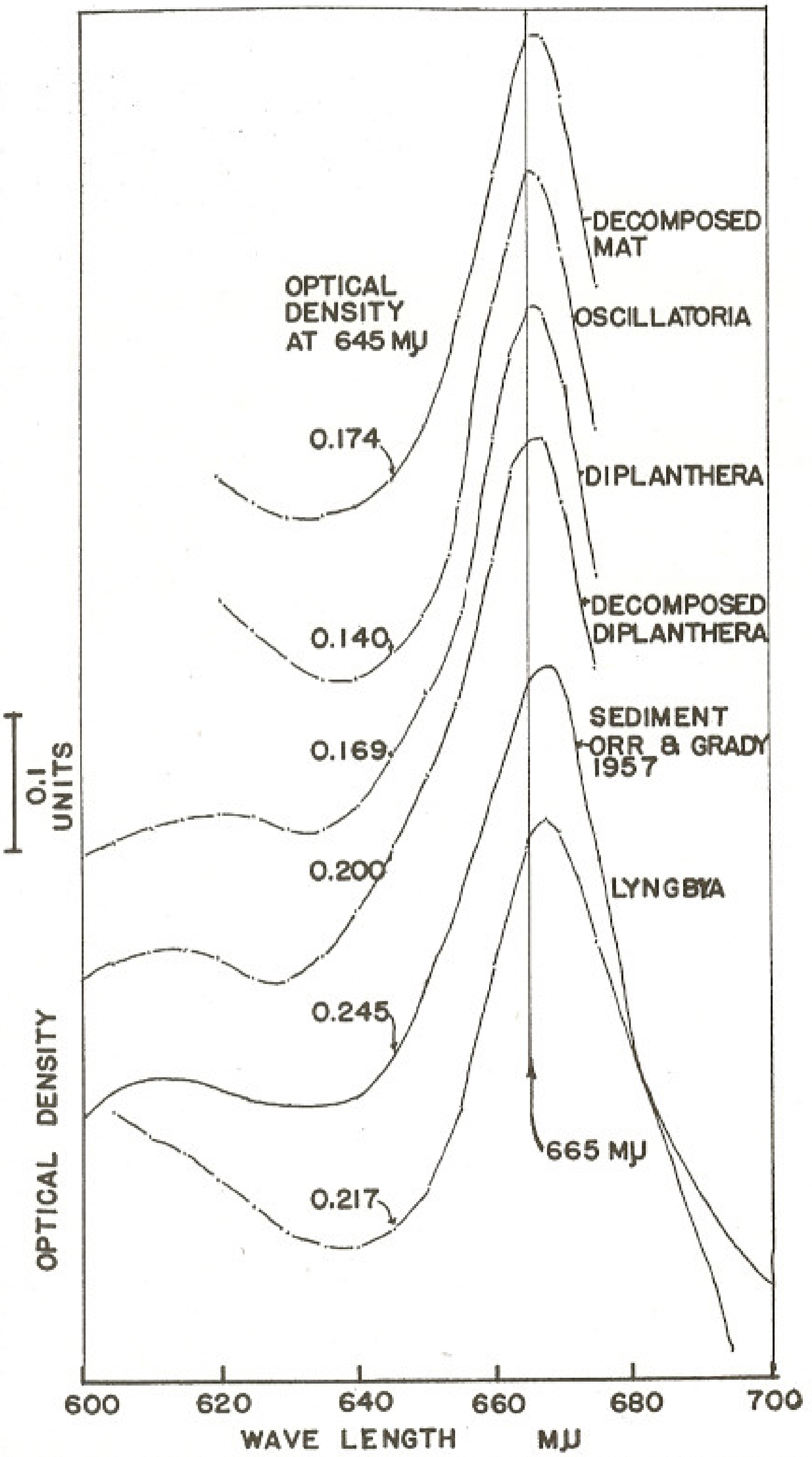

Fig. 1. Absorption spectra of living and decomposing aquatic plants. Beckman DU Spectrophotometer at slit width 0.04 mm. The peak optical density of each curve is adjusted to optical density 0.5 for comparison.

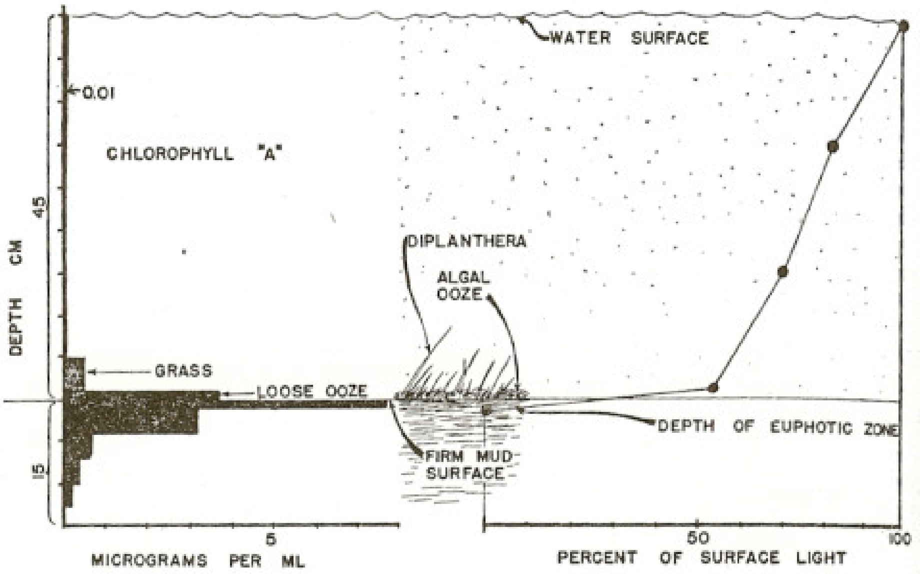

FIG. 2. Vertical stratification of chlorophyll "A" and light intensity (Dec. 29, 1957) in the shallow water and ooze of the upper Laguna Madre, Reds Fish Camp, Texas.

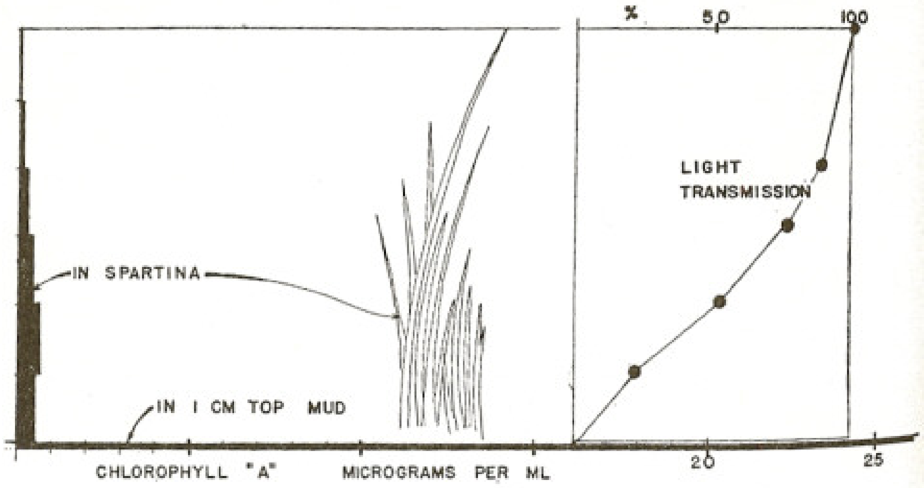

FIG. 3. Vertical stratification of chlorophyll and light intensity in the marsh grass, *Spartina sp.* and the mud surface of Aransas Bay, Texas, March 21, 1958.

Data on light intensity and chlorophyll "A" in the shallow, grassy, bay bottom of the upper Laguna Madre of Texas and in an area of sparse marsh grass near Port Aransas are given in Figures 2 and 3. The depth of the euphotic zone was measured as about 1 cm. deep into the bottom ooze. A submarine photometer was pressed into the ooze in order to determine the depth of penetration of effective light intensity. After collecting a core in a plastic pipe pressed into the mud, the core was frozen and extruded from the pipe. Then one cm. sections of the top were cut off for chlorophyll extraction. There are very large amounts of non-functional chlorophyll below the euphotic zone in the mud (Fig. 2). These deep layers are not assumed, a priori, as dead and incapable of photosynthesis, but one can assume that if no appreciable light penetrates, there is no effective

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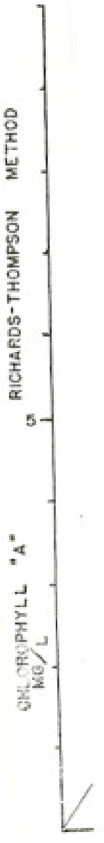

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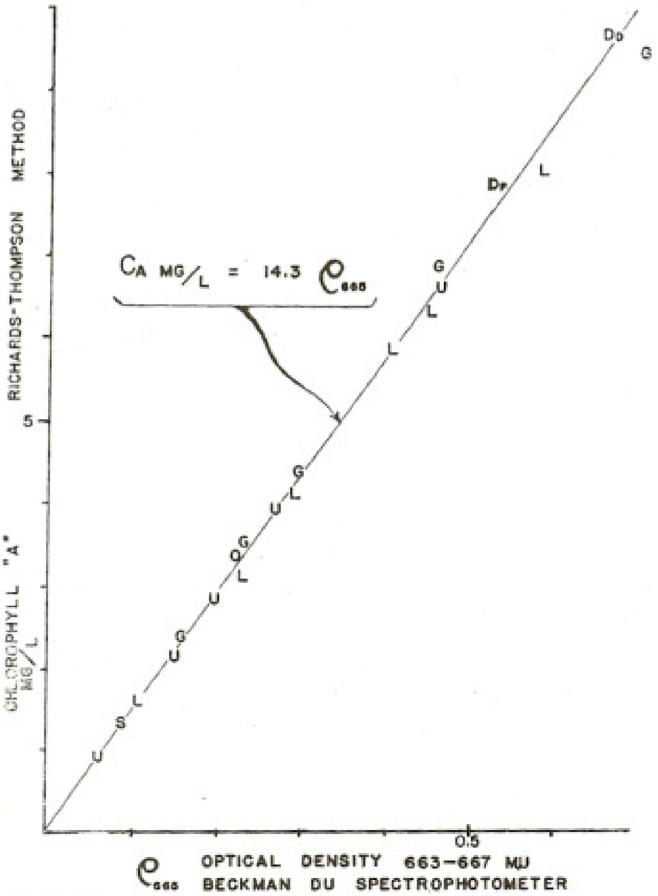
production. One must always consider the possibility of vertically migrating sediment algae, that migrate below the euphotic zone for part of the day (Aleem, 1950). Non living chlorophyll is a usual constituent of freshwater and marine sediments (Vallen-yne, 1955). Large amounts of non-living chlorophyll also occur below the euphotic one in deep layers of marine and freshwater bodies.

CHLOROPHYLL "A" DETERMINATION FROM OPTICAL DENSITY MEASUREMENTS AT ONE WAVE LENGTH

The measurement of the optical density of chlorophyll in acetone extracts at three ivelengths is time consuming where large series are needed for meaningful averages. mparisons of results based on measurements at 665 millicrons were made with results m measurements of three wavelengths. Widely different plant materials including e-greens and higher plants were extracted and measured in the Beckman DU spectro-tometer. Each extract was measured at 3 wave lengths and the values computed as orophyll "A" plotted against the optical density determined at 665 millimicrons (Fig. The close alignment of points indicates that the 3 wave length procedure is unneces-



. 4. Chlorophyll "A" concentration determined by the Richards-Thompson method using read- at 3 wavelengths as a function of optical density at one wavelength (665 millimicrons). Beckman Spectrophotometer, slit width, 0.04 mμ. U, *Ulva fasciata;* L, *Lynbya sp.;* G., *Gephortia mitchelae; Oscillatoria sp.;* D_f, fresh *Diplanthera wrightii* blades; D_d, decomposed *Diplanthera* blades; S, omposed sedimentary material containing blue green algal mats.

sary considering the other greater sources of error. Where optical densities are read with a 1 cm. optical light path in a narrow band pass spectrophotometer, the Richards and Thompson Chlorophyll "A" procedure is abbreviated in equation (2) as follows:

$$\text{Chlorophyll A in mg./l} = 14.3\ d_{665} \quad (2)$$

CHLOROPHYLL "A" DETERMINATION ON A PORTABLE SPECTROPHOTOMETER WITH BROAD BAND PASS

The Bausch and Lomb "Spectronic 20" spectrophotometer has been found useful for determinations of chlorophyll because of portability, reliability, and relatively low cost ($240) permitting semi-field use. The width of the spectral band pass is given by the manufacturer as 20 millimicrons. Thus when the wave length is set on 665 millimicrons, light between 653 and 673 millimicrons is passing into the extract tubes. Thus the range of absorption is broad enough that the amount of Chlorophyll "B" present can affect Chlorophyll "A" determinations. Chlorophyll "B" has an absorption peak at about 645 millimicrons not far from the 653 millimicron light.

A series of measurements was made on both the Beckman narrow band pass instrument and on the broad band pass Bausch and Lomb instrument. In Figure 5 the Chlorophyll "A" figures with the Richards-Thompson method are plotted against the optical density readings at the single 665 millimicron setting on the Bausch and Lomb instrument. Data for a red, green and blue-green alga differ considerably. Readings on broad band pass instruments differ from narrow band pass measurements even when there is but one pigment present. The average per cent absorption over the 20 millimicron range must be on the average less than the per cent absorption in a 5 millimicron band pass located on the sharp peak of absorption.

Thus when the Bausch and Lomb instrument is used for field use it is desirable to convert optical density measurements into Chlorophyll "A" values with curves like those in Figure 5. A calibration graph determined for higher plants should not, for example, be used to compute Chlorophyll "A" values in extracts from red algae.

In the chlorophyll procedure of Hogetsu and Ichimura (1954) chlorophyll is converted into phaeophytin with acid. In the chlorophyll procedure of Creitz and Richards (1955) magnesium carbonate is used to prevent the decomposition of chlorophyll into substances like phaeophytin. In these considerations a shift or possible shift of the red peak of chlorophyll is involved. If a wide band spectrophotometer is used all of the compounds with peaks in this area are measured, and the conditions of handling may not be so crucial. For field use in a wide variety of types of plant material, simplicity in chemical procedure is essential. Where the largest errors are likely to be ones of sampling, rapid methods which permit replications are desirable.

Since the roles of Chlorophyll "B" and "C" in photosynthesis are not adequately known, it is not possible to state whether or not plants with much Chlorophyll "B" or "C" will have a different assimilation number relative to Chlorophyll "A" in comparison to plants without these pigments. Assimilation numbers in this paper are computed relative to Cholorphyll "A" only.

NOTES ON EXTRACTION

The extraction of Chlorophyll "A" from widely divergent materials for ecological purposes, requires a variety of extraction methods. Large, leafy plant itssues are passed through a meat grinder, slurried in water, aliquoted, partially dried, and extracted with

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FIG. 5. Chlorophyll "A
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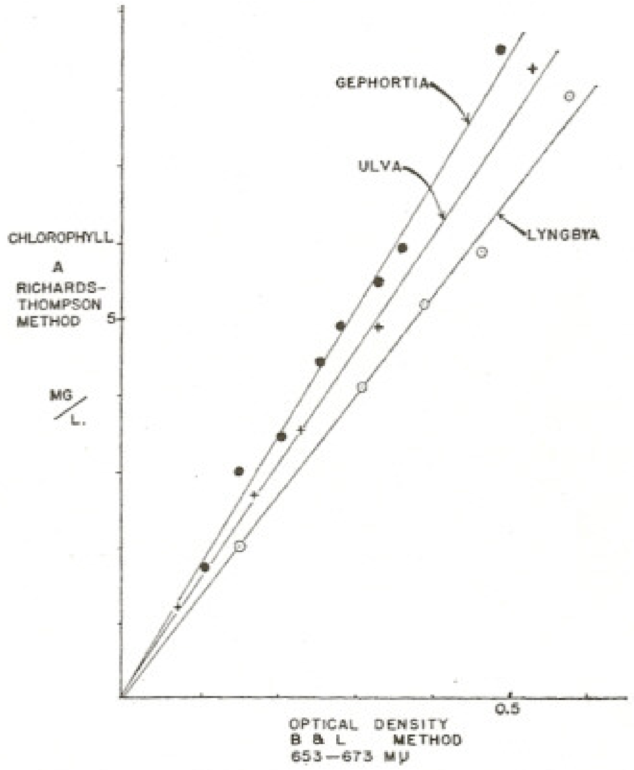

FIG. 5. Chlorophyll "A" determined with the Richards and Thompson method on the Beckman DU spectrophotometer as a function of optical density at 663 millimicrons and 1.17 cm. light path on a Bausch and Lomb "spectronic 20" spectrophotometer. *Ulva fasciata*, a green alga; *Gephortia mitchelae*, a red alga; and *Lyngbya major*, a blue-green alga.

90 per cent acetone. Discs from rain forest leaves were punched, bruised, placed in 10 cc. acetone (90%) in vials, and extracted completely in 24 hours in a refrigerator without further grinding. Some plankton samples on millipore filters extract readily without mechanical damage to cells (Creitz and Richards, 1955). Other algae require grinding in mortar and pestle with clean sand. Corals and calcareous algae were cut with hacksaw and ground in a mortar.

Rocks in streams were extracted by immersion in pans of acetone accompanied by brushing by McConnell (1958) and in class sampling work at Duke in 1956. Freeze drying of leaves was effective where preservation was necessary and where greatest accuracy was desirable.

Some algae are sufficiently bruised in a Waring blendor for subsequent extraction. Others resist extraction. Species of *Prasiola, Ulva, Cladophora, Thalassia, Diplanthera, Phormidium* and *Enteromorpha* were especially resistant. With larger tissues, observation of the residual color may be used to ascertain if most of the extraction has taken place. With tiny plankton cells on a millipore filter, the lack of extraction may be readily overlooked. In one extraction involving a species of *Chlorella*, only a small fraction of chlorophyll was removed from the filter residue until grinding was done with sand.

Extraction is made with 90 per cent acetone. If 100 per cent acetone is used to dissolve millipore filters, a part of the filter goes into solution which precipitates as a milky turbidity later when the solution is adjusted with water to 90 per cent acetone. Ideally final extracts are in 90 per cent acetone. Final stages of extraction are usually carried on for 24 hours in a refrigerator in the dark.

VALIDITY OF RICHARDS AND THOMPSON'S PROCEDURE FOR 90 PER CENT ACETONE

In developing the chlorophyll assay method (equation 1 in this paper) Richards with Thompson (1952) cite the work of MacKinney (1941) and Zscheile, Comar, and MacKinney (1942) and adopt extinction coefficients for use in 90 per cent acetone solutions. Richards with Thompson (1952) prepared Chlorophyll "A" from *Macrocystis* with chromatographic methods and used the coefficients of the previous authors for determining the grams of chlorophyll represented by the extraction. MacKinney made measurements at 663 millimicrons whereas Richards used his new curve to determine absorbancy at 665 millimicrons. In actuality, the extinction coefficients reported by Zscheile and co-workers and MacKinney are for 80 per cent acetone solutions of pigments. The effects of changes of solvent on the spectrophotometric properties of plant pigments have been widely discussed elsewhere (Franck and Loomis, 1950; Rabinowitch, 1951). A series of experiments was run by Walter Abbott to test the effect on absorbance of a change of solvent from 80 per cent to 90 per cent with pigments from terrestrial plants. (This was not a test of extractability, but a test of the basis of Richards and Thompson's equation.)

Small portions of fresh leaves from a variety of plants were extracted with 10 ml. of neutral, redistilled reagent grade acetone. Extraction was carried out in the dark at 5° C. When extraction was completed, two 4 ml. aliquots were withdrawn. With a microburette, these were adjusted to 80 per cent and 90 per cent acetone contents by addition of distilled water. Correction for nonideal behavior of acetone water mixtures was made from an empirically determined chart of volume relationships. Samples were then cooled and stored briefly in the dark until spectra could be scanned on the Beckman DK recording spectrophotometer. Data from these measurements are in Table 1.

TABLE 1
Absorbance Values
(Optical Density in 1.0 cm. Light Path)

Species	663 mu		645 mu		630 mu	
	80%	90%	80%	90%	80%	90%
Catalpa bignoniodes	0.600	0.649	0.264	0.279	0.170	0.166
Quercus phellos	0.441 0.568	0.474 0.581	0.199 0.258	0.219 0.268	0.113 0.145	0.124 0.147
Rhus glabra	0.410 0.664	0.434 0.718	0.176 0.303	0.189 0.332	0.100 0.167	0.103 0.189
Celtis occidentalis	0.538 0.952	0.564 0.956	0.244 0.427	0.252 0.447	0.140 0.248	0.140 0.228
Ulmus americana	0.286 0.252	0.302 0.356	0.131 0.133	0.135 0.154	0.082 0.084	0.082 0.088
Quercus virginiana	0.890	0.972	0.333	0.344	0.189	0.188
Juniperus mexicanus	0.366	0.502	0.164	0.207	0.085	0.117
Cercis canadensis	0.517	0.558	0.175	0.209	0.082	0.101
Unidentified seedling	0.568	0.581	0.227	0.226	0.110	0.107

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Accompanying the change of solvent from 90 per cent acetone is a 6 per cent lowering of absorbance at 663 millimicrons and at 645 millimicrons. Data taken by the Richards and Thompson method should be corrected by multiplying absorbances at 663 millimicrons and 645 millimicrons by 0.94. Equation (2) above thus modified becomes equation (3) below:

$$\text{Chlorophyll "A" in mg/1 of 90\% acetone} = 13.4\ d_{665} \quad (3)$$

With the Bausch and Lomb broad band pass instrument, however, the composition of the extract is not so important since part of the solvent effect is a change in wave length of the peak of the spectrum. McConnell (1958) found relatively minor effect of changing water composition.

Steady State Energetics of Input-Output Systems in Which the Input Energy Arrives as Packets of Fixed Energy Content; The Cannon-Ball Catcher

In order to better understand the energetic coupling of biochemical machines to the steady inflow of photons of light, it is convenient to describe the cannon-ball catcher (Fig. 6). Although the machine is an analogy, its energy aspects are thought to be similar to those of primary production systems. It is possible to erect hypotheses which account for the behavior of input-output systems containing chlorophyll with respect to light, temperature, nutrients, and other factors. That the behavior of chlorophyll adaptation seems logical when compared with a cannon-ball catcher is at least an aid to the memory. In the discussion that follows the behavior of chlorophyll is related to mechanisms of self regulation believed to exist in plants at a higher level of organization than single reactions of photochemistry and photosynthesis.

The cannon-ball catcher machine is a coupled input-output system like those described in a previous paper (Odum and Pinkerton, 1955). Energy arriving in the form of cannon-balls is caught by cups on a turning wheel of the cannon-ball catcher. The input energy system thus receives a steady flow of energy in discontinuous similar packages. After catching a ball, a receptor to be used again must be revolved through a cyclic process requiring a discrete time. The input system is geared by a pulley system and a fly wheel to a machine for doing work. Therefore, a discontinuous energy input drives an output that may have a more regular power distribution with time. A review of the possible kinds of biochemical reactions by which such input-output systems might function is given by Strehler (1958).

There are several similarities between a cannon-ball catcher and a photosynthetic machine. A plant receives discontinuous photons just as the catcher receives cannon-balls, and is geared to a chemical machine that produces organic, synthetic work. The number of cups per machine is comparable to the concentration of chlorophyll per chloroplast. A cyclic biochemical process is necessary for maintaining chlorophyll "A" in receptive state (see flashing light research: Rabinowitch, 1956: 1433) just as the cups on the wheel must be revolved for reuse. As discussed previously (Odum and Pinkerton, 1955) maximum power output is gained with a particular and optimum force adjustment between input and output systems. It is likely that plants contain mechanisms for maintaining optimum adjustments, and these are established by natural selection.

Consider a situation with a steady influx of cannon balls. The steady torque developed by the impinging balls can be varied by changing the number of cups on the catcher wheel. With more cups more balls are caught. In this way the input drive can be adapted for a given output load so as to provide the maximum power. The rest of the cannon-balls can pass uncaught to be accepted by another catcher machine below.

Similarly in photosynthesis one can imagine that the number of receptive chlorophyll molecules provided can be controlled in order to maintain the ideal photochemical drive to the respiratory system. Changes in light or in factors affecting respiratory system rates are likely to be accompanied by changes in chlorophyll in order to maintain the adjustment within the chloroplast. Such adjustment prohibits acceptance of too many or too few photons. Conservation of photons not only maintains proper load ratios in the immediate biochemical system but contributes to the maximum output of cells just below.

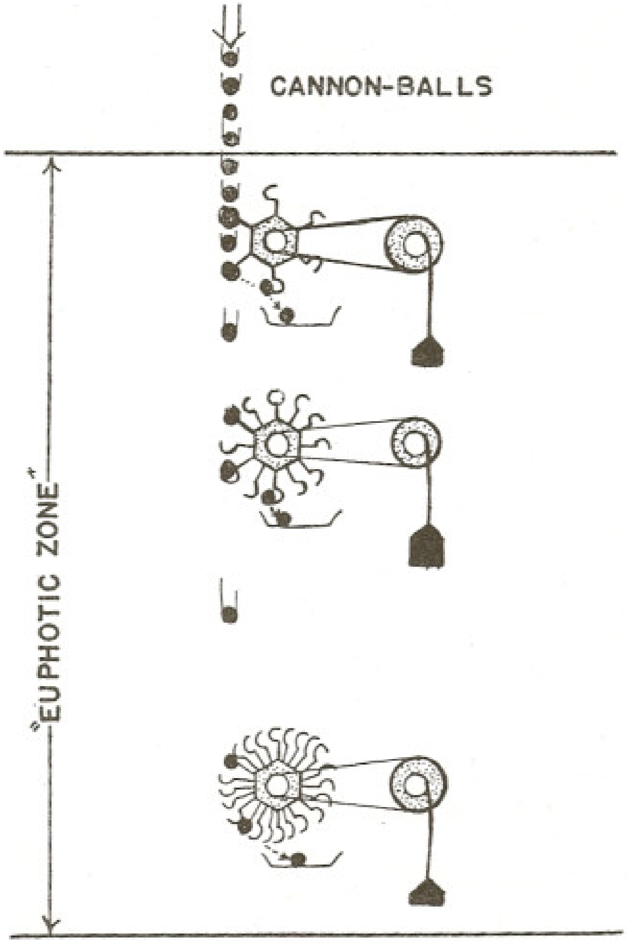

FIG. 6. Three cannon-ball catcher machines in vertical sequence. The upper machine is adapted to the area of great flux of cannon-balls because relatively few cups are protruding; the lower machine is adapted to the area of few cannon-balls with a large number of cups in position.

According to the theory of energy adaptation, outlined in the text, successfully surviving photosynthetic systems adapted in nature have mechanisms to change number of cups in order to adapt to the rate of energy influx and so as to develop maximum power output of the entire population throughout the euphotic zone.

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The total yield of the whole euphotic zone is thus higher. Maximum yields are possible if a multi-layered reception system is active.

If the theory of optimum input-output adjustment of chlorophyll is correct, then the chlorophyll fluorescence as an input energy flow meter (Katz, 1949) is likely to be maintained in fairly constant ratio to photosynthesis under adapted circumstances. A correlation of the fluorescence of live chloroplasts and photosynthesis does exist (Rabinowitch, 1951: 819; Brugger, 1957).

The fluorescence of living chlorophyll systems may have some analogous similarity to the loss of energy that occurs when a cannon-ball strikes the cups of the catcher machine. Both phenomena are likely to be accentuated when the cycles of the receptive material (cups or chlorophyll) are being retarded and are not dispersing energy at optimum speed. Katz (1949) found increased fluorescence with artificially retarded photosynthesis.

Discussion of chlorophyll, light, and other factors follow with reference to energetics and input-output systems.

The purpose of the cannon-ball picturization is to make clear the hypothesis that photosynthetic systems in order to maintain maximum power output can regulate the input power by regulating the chlorophyll.

Summary of Ecological Factors Affecting Chlorophyll and Assimilation Number

Reports from the literature on the spatial and temporal patterns of chlorophyll in natural communities are not uniform. Nor do the data from the experimental literature at first suggest simple relationships between environmental factors, chlorophyll, and assimilation. In the following paragraphs an attempt is made to summarize and account for the adaptive behavior of systems containing chlorophyll.

LIGHT INTENSITY AND THE CHLOROPHYLL CONCENTRATIONS IN A *Part* OF A COMMUNITY

Consider only plants growing under conditions of illumination to which they are adapted for effective competition. Such adaptation may be in the laboratory or outdoor situations. In adapted condition the chlorophyll of single leaves, cells, and other community parts tends to be diminished as the chloroplasts adapt to increasing light intensity (See various authors cited by Rabinowitch, 1956: 1261). However the effectiveness of adapted chlorophyll for photosynthesis (i.e., assimilation number) increases with light intensity. (See examples cited by Rabinowitch, 1957: 1262). With less chlorophyll per cell a larger part of the incident light passes through to the next layer of plants so that the total energy absorbed for photosynthesis in the top layer may be less. Consequently single cells or leaves may have lower, equal, or greater total photosynthesis in brightest light. It may be a misnomer to refer to diminished output of naturally adapted cells in bright light as saturation in any sense of malfunction. The effect of adaptation to intense light is to increase the assimilation number of the top cells in spite of decreasing chlorophyll concentration. In a yellow variety of *Sambucas* Willstatter and Stoll (1918) measured an assimilation number of 84 gm./gm./hr. In contrast, shaded cells of a community possess higher chlorophyll concentrations and lower assimilation numbers. At light intensities for maximum photosynthesis of single cells, assimilation numbers of 7.4 gm./gm./hr. (range, 4 − 12 gm./gm./hr.) are found (Ryther and Yentsch, 1957).

These relationships of assimilation number, chlorophyll, and light have been shown by many authors. For example, Phillips and Myers (1954) presented a graph for *Chlorella* which shows diminishing chlorophyll per cell with adaptation to greater light intensity. Ichimura (1958) reports data on lake plankton in field conditions with rising assimilation numbers correlated with increasing light intensity for three seasons. Assimilation numbers were about 1 gm./gm./hr. with 3 per cent light rising to 7 gm./gm./hr. at 60 per cent light.

The adaptation found for chlorophyll and assimilation in bright light may be compared to the cannonball-catcher in a zone of numerous flying cannonballs. In order that the same torque be exerted upon the output machinery, it becomes necessary to diminish the number of cups on the wheel. An overloaded system runs too fast for most effective use of the energy. By reducing the number of cups the top machine works at optimum and the uncaught balls pass below to the next cannonball machine for effective use there. The decrease in number of cups in this situation may be compared to decrease in chlorophyll in bright light. With plenty of cannonballs for the available cups, there is a large work output per cup just as there is a large assimilation per unit chlorophyll.

The large chlorophyll content of cells adapted to the shade may be compared to the numerous cups on the cannonball-catcher. Many cups are needed to maintain enough power output for survival. With few balls received the output work per cup is small just as the assimilation per unit chlorophyll is small in the shade. Efficiency is large in a slowly turning wheel because there is a greater potential energy difference maintained between incoming and acceptor energy states. The efficiency of the slowly turning wheel may be compared to the high efficiency that occurs with low rates of assimilation of plants adapted and operating in the shade (Nihei, Sasa, Miyachi, Suzuki and Tamiya, 1954).

Gessner (1949) adapted lake plankton for five days in light and dark conditions. The plankton initially had an assimilation number of 1.4 gm./gm./hr. At the end of the experiment the shaded plankton had an assimilation number of 0.1 gm./gm./hr. whereas the plankton in bright light had an assimilation number of 5.8 gm./gm./hr.

Marshall (1956) showed relative increase of marine plankton chlorophyll in bottles in shade relative to bottles at the surface. Manning and Juday (1941) found higher assimilation numbers in hypolimnetic plankton. Sargent (1940) showed twice as much chlorophyll in shade adapted *Chlorella* as in light adapted algae, although the light adapted algae had the greatest yields. He reviewed the work of five earlier authors with similar results.

In Sargent's work the chloroplasts in the sun had less chlorophyll present. Gessner (1955) described thinner chloroplasts in *Spirogyra* in light adapted plants. Movements of the chlorophyll and chloroplasts so as to transmit more light under bright light conditions are summarized by Rabinowitch (1951:681).

LIGHT INTENSITY AND CHLOROPHYLL IN THE WHOLE EUPHOTIC ZONE OF A COMMUNITY

The total chlorophyll which develops under a square meter tends to absorb most of the available light. A thick zone of chlorophyll may develop which is light adapted at the top and shade adapted below. The greater the light intensity is at the top of the community the greater the total amount of chlorophyll which develops within the euphotic zone. For a whole lake Ichimura (1958) found increasing assimilation numbers as chlorophyll increased.

The chlorophyll per unit area thus increases with light intensity under adapted condition even though the chlorophyll per cell may decrease in the upper layers. An apparent paradox results. Communities adapted to bright light may seem pale from above and yet may contain more chlorophyll. The greenest appearing communities are not necessarily the most photosynthetic or the greenest in extraction. Pale appearing communities, however, do not necessarily have additional chlorophyll below, for there are other limiting factors such as nutrients.

The effectiveness of the total chlorophyll of the whole euphotic zone increases with incident light intensity. Increase of light intensity causes bright adapted cells with high assimilation numbers to develop on top of and in addition to the cells present under lesser light intensities. Thus the overall assimilation number increases with incident light.

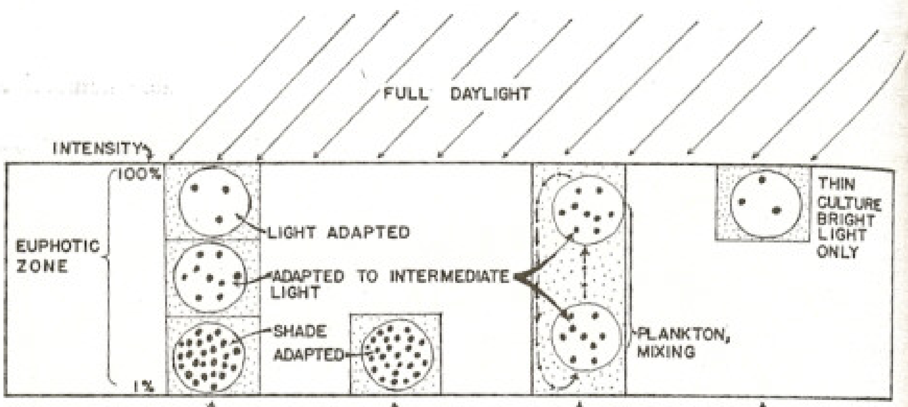
Since in whole communities both chlorophyll and assimilation number increase with light intensity, total photosynthesis increases with light intensity even under conditions of full daylight. The whole zone therefore in photosynthetic response to bright light differs from the behavior of single cells, leaves, or small plants. Parts of communities have optimum light intensities for maximum photosynthesis. See numerous examples in Rabinowitch (1951:964) and Gessner (1955). Whole naturally adapted communities have maximum photosynthesis at maximum light intensity. Examples of communities (whole euphotic zone) without maxima in their photosynthetic curves (per area) with light are: mass algal culture (Burlew, 1953: 17); Silver Springs (Odum, 1957); pine tree (Kramer, 1958: 163); aquatic plants (Gessner, 1955: 86); marine waters (Marshall and Orr, 1929; Jenkins, 1937; Ryther, 1956b); *Cabomba* (See Rabinowitch, 1951: 968); lakes (Ichimura, 1958); Lake Erie plankton in seasonal comparisons (Verduin, 1956); and surface algae (Manning, Julay, and Wolf, 1938). Takeda and Maruta (1956) found light saturation in individual rice plants but not in communities of rice plants.

In plant cells in which there is an optimum light intensity for maximum photosynthesis, a midday depression in production may occur (Rabinowitch, 1951:873). In an adapted community with a full depth of chlorophyll, midday depression is not expected. Any tendency for saturation of surface cells is more than compensated for by additional photosynthesis of the deeper cells receiving light only during the brightness of midday.

Because shaded communities are more efficient (not more productive) than light adapted zones, assimilation and assimilation numbers do not diminish on cloudy days as much as the light intensity. Steeman-Nielsen (1954), Verduin (1956), and Edmondsen (1956) have reported smaller deviation in community photosynthesis than expected from changes in light intensity. Community efficiency increases as light intensity diminishes (Wassink et al., 1953; Odum and Hoskins, 1958).

FOUR TYPES OF CHLOROPHYLL ADAPTATIONS TO LIGHT BY PRODUCER SYSTEMS

The general principles concerning chlorophyll states and light in plant communities can be summarized by considering whole natural communities and laboratory experiments as belonging to one of four types pictured in Figure 7. The difficulty encountered



COMMUNITY TYPES	STRATIFIED	SHADED	MIXING	ALL BRIGHT
TOTAL AREA CHLOROPHYLL "A" GM/M²	0.4-3.0	0.001- 0.5	0.02- 1.0	0.01 – 0.60
COMMUNITY ASSIMILATION RATIO GM/GM/HR	0.4 - 4.0	0.1-1	1-10	8–40
EFFICIENCY OF VISIBLE LIGHT ABSORBED %	1-8	10 - 30	1-5	0.1 - 3
PHOTOSYNTHESIS GM/M²/DAY GROSS	1–60	0.01–1.0	0.5–30	0.5–10

Fig. 7. Four types of chlorophyll adaptations to light by producer systems. The concentrations of chlorophyll are indicated diagrammatically by the density of dots in the circles. Estimates of chlorophyll, assimilation number, efficiency, and community photosynthesis are derived from Table 2 and from the literature.

in recognizing light adapted patterns in nature is attributed to the interplay of other factors on the vertical distribution of chlorophyll.

1. *Stratified community.* There are light and shade adapted portions. Chlorophyll per cell increases downward. All of the incident light is effectively used. Assimilation number decreases downward but the overall assimilation number of the community is high. The overall efficiency of photosynthesis is also high. The total chlorophyll per area is large but may not appear so from the top view. Such communities are the most productive of any yet measured. Forests and benthic communities are examples of this type. Some stratified, quiet waters develop vertical stratifications of planktonic algae with similar patterns.

2. *Shaded Community.* A community developing and becoming adapted to low light intensity may be considered to be the same as the lower portion of a stratified community in full daylight. In other words, the shaded community lacks the light adapted parts. It is relatively high in chlorophyll concentration but has less than the stratified type although it may appear much greener. With lower light intensities efficiency is greater but with so little light the total photosynthesis is less. The excess chlorophyll needed to gather light in shaded conditions is not in effective continual use and the assimilation

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mbers are small. Such communities may occur in winter seasons, in caves, and in most oratory work where light intensities are rarely as bright as full daylight. Many misding ideas have developed concerning nature from work with shade adapted comnities. Many popular writers overestimated the possible yields of algae by considers representative the high efficiencies found at low light intensity.

3. *Mixing Community.* In turbulent upper waters of lakes and oceans at some seasons, principal producers are moved up and down and are subjected to alternating conions of shade and light. Cells move from full daylight to half daylight in a matter of minute or two where mixing is effective. (See discussion of the diffusion of oxygen dum and Hoskins, 1958). Waters in the upper zones of aquatic environments also reive flashing light due to wave effects at the surface in diffracting and reflecting light. pecially in the sea such cells cannot become adapted to either shade or bright conions. It is possible that plankton cells of this type are adapted to intermediate light. might be expected, such cells have intermediate chlorophyll concentrations and similation numbers (Table 2 and Fig. 7). If the euphotic zone is spread over any apeciable depth, the water absorbs a large proportion of the potentially usable light as eeman-Nielsen (1957) has discussed. Such communities may thus receive less total ght, develop less total chlorophyll per area, and yield less total photosynthesis. Ryther 1956a) was unable to find much light and shade adaptation in *Dunaliella* in contrast the adaptation in other species found by many workers. Ryther found assimilation umbers of only 1–5 gm./gm./ hr. in contrast with higher numbers in other data for ight adapted cells. However, no adaptation was attempted above 1500 ft. candles whereas daylight is usually greater than 10,000 ft. candles. Whether usual plankton algae are capable of becoming light and shade adapted cannot yet be generalized.

In a rain forest in the intermediate depths, light is rather uniform due to the scattering of light by the leaves (unpublished data of Odum, Abbott, and Selander). Such forest leaves may also be adapted to intermediate light intensities. As the leaves are rustled by the breeze on bright days, flecks of bright sunlight momentarily illuminate the lower layers. Thus forest leaves on a sunny day are exposed to considerable variation of incident light intensity, and adaptation to one light intensity may be difficult. Steeman-Nielsen (1957) presents a discussion of light and chlorophyll in forests and waters.

4. *Thin culture with all bright light.* In many laboratory cultures especially those with lights inside the containers, there is no part of the system where there is shade. Such cultures, which are never allowed to get so dense as to produce their own shade, may be visualized as the upper part of a full stratified community. Unfortunately, generalizations have been made about such cultures without realization of their specialized nature. One may overestimate potential yields if one extrapolates with the high assimilation numbers of light adapted cultures.

A bright adapted community has low concentrations of chlorophyll per volume of cells and has very high assimilation numbers. Efficiency of use of the light absorbed is low at high light intensity. Total area based photosynthesis may be higher than in the shade adapted community but is less than in the two types of communities that represent full euphotic zones. Such cultures are particularly misleading about chlorophyll since the assimilation numbers are much higher than in full depth communities (20 gm./gm./hr.; Ryther, 1956a). Such communities occur in nature where only thin vegetation can develop sometimes on surfaces of rocks, water, or in new colonization. Agriculture is often of this type. Sunflowers have high assimilation numbers (8–16 gm./gm./hr.; Willstatter and Stoll, 1918).

LIMITING MATERIAL REQUIREMENTS AND CHLOROPHYLL

Consider next plants growing with adequate light but sub-minimal rates of supply of the materials needed for photosynthesis and growth. The literature of plant physiology (Hill and Whittingham, 1955, for example) and plant ecology (Harvey, 1955, for example) are full of cases in which limiting factors are demonstrated. Chlorophyll concentrations diminish when plants adapt to maintain minimal existence in limiting environments. Physiological studies indicate that subminimal amounts of different limiting factors including iron, nitrogen, potassium, magnesium, and water induce lowered chlorophyll as summarized by Rabinowitch (1945: 427; 1956: 1267). The operation of nutrients in stimulating increase of chlorophyll in whole community systems also has been frequently noted. For example S. Conover (1956: 85) showed the effects of nutrients on chlorophyll of plankton populations in bottles, and Edmondson (1955) showed increased chlorophyll with fertilization in a tank. No attempt is made to separate instances where the increased chlorophyll is within cells already existing from those where new cells form.

If the output machinery is limited by some factor, a reduction of input torque is necessary to maintain the proper load ratio and to allow energy to pass to lower levels of the community where limiting conditions are possibly equal or less restrictive. The rate at which energy is entering may be diminished by the elimination of some of the receptors in each machine. In the machine the decrease in receptors is an adaptation to the mechanical requirements of the input-output gearing. The disappearance of chlorophyll in environments unfavorable for photosynthesis need not be described as pathological in plants surviving in such conditions, for the diminished chlorophyll may be an adaptation of input to the externally limited rates of output for purposes of economy. Just as the output per cup remains high so in these limitations the assimilation per unit chlorophyll remains high. The high assimilation numbers of yellowing autumn leaves (Willstatter and Stoll, 1918) may be from a diminishing supply of raw materials at the leaf site.

Many studies have related the higher chlorophyll content of generally rich eutrophic waters to high nutrient levels (Deevey, 1940; Ichimura, 1956). However, some of these studies accentuate the lesser chlorophyll of oligotrophic waters by expressing data on a volume of water basis. Thus clear water has a deeper euphotic zone and less chlorophyll per volume even when chlorophyll per area is the same. Such regional comparisons should be made on an area of community basis.

The nutrient factor is affected by temperature. At high temperatures there is a rapid regeneration rate in respiratory systems of the community so that a steady supply of nutrients is not as important.

TEMPERATURE, TISSUE SIZE, AND CHLOROPHYLL

There are two factors which affect chemical reaction rates and as a result affect the chlorophyll content of communities. First consider temperature.

Although the initial photochemical events of photosynthesis are physical in nature and little subject to temperature, most of the photosynthetic machinery is biochemical,

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metabolic, and made of reactions which follow laws of chemical reaction rate. As the temperature rises, the rates of reaction and recycling of materials increase. Materials are released by respiration more rapidly also. At high temperatures, therefore, less mateials are needed for the same flux of energy because materials are reused more often. In photosynthesis chlorophyll is connected to an action and recovery cycle that is chemical in nature, and its synthesis is chemical. Consequently, at higher temperatures less chlorophyll may be needed at any instant because of the greater possible turnover rate. Even though the chlorophyll functions in a temperature independent photochemical action, the amount of chlorophyll is regulated by a temperature dependent system in order to maintain optimum input-output adjustment. Assimilation numbers may be larger (Rabinowitch; 1956: 1272). Willstatter and Stoll (1918) found slight increase in assimilation number from 25° C. to 30° C. Myers and Kratz (1955) found less chlorophyll developed at higher temperatures in *Anacystis*. With less materials to maintain, cells may be smaller for the same job at high temperatures. Next, consider tissue size as a factor.

It is now known in plants that in photosynthesis as well as in respiration smaller cells have greater turnover (Margalef, 1957; H. T. Odum, 1956; E. P. Odum, Kuenzler, and Blunt, 1958). The metabolism per gram inversely varies approximately as the ⅓ power of the linear thickness of the tissue. It has been postulated that diffusion properties are responsible for the greater metabolic rate of smaller cells because the power of diffusion per gram to carry materials into and out of the cell varies as the ⅓ power of the thickness. In any case the smaller the plankton cell or the thinner the leaf tissue, the more rapid is the possible metabolism per cell. In small cells with more chemical respiratory turnover per gram, more chlorophyll per gram (or per volume) is necessary to maintain proper input torque than in large cells, but as in temperature effects, it may again be postulated that conditions permitting rapid turnover will similarly permit the cells to maintain higher assimilation numbers and less chlorophyll for the same photosynthetic flux. The respiratory output rate by this hypothesis controls the adjustment of chlorophyll for proper input-output stress.

If these postulations are correct, higher assimilation numbers may be expected in smaller cells and at higher temperatures. In terms of input-output systems any modifications of the circulating machinery which permits a more rapid turnover, will permit fewer receptors to catch the same number of energy units.

In Table 2 are presented data on chlorophyll in communities. There is a tendency for higher assimilation numbers and smaller chlorophyll contents per area in plankton communities than in communities made up of plants with thicker tissues. In *Chlorella* smaller individuals have more chlorophyll per gram and greater assimilation numbers (Tamiya *et al.*, 1953). In the Laguna Madre of Texas (Table 3) assimilation numbers are higher in the plankton than in the benthic plants beneath.

Chlorophyll in Partially Heterotrophic Plants

In completely heterotrophic plants chlorophyll may be absent, but in some partially heterotrophic organisms there may be chlorophyll based nutrition as well as heterotrophic based energy intake. At the base of a growing aquatic plant, blades in the tissues recently formed from meristematic growth, and in *Euglena* cultures placed in the dark, there are cells which may have photosynthetic capacity when placed in the light at a later time, but which are living off imports of organic food. Such tissues apparently have

Table 2

Chlorophyll and Assimilation Number in Communities

	Euphotic Zone Chlorophyll "A" Gm./M.^{2}	Assimilation[a] Number Oxygen gm./gm./hr.
PLANKTON COMMUNITIES (Not including bottom plants)		
Fertilized tank, marine, 1.5 M deep (Edmondson and Edmondson, 1947)	0.030	7
English Channel, 70 M deep (Jenkins, 1955)		
Summer and winter	0.20	....
Spring blooms	1–3	....
Long Island Sound (Riley, 1956; Conover, 1956)	0.1–0.6	1–3
Phosphorescent Bay, Lajas, Puerto Rico, 3.7 M deep January 23, 1957	0.033	4
Baffin Bay, Texas, 1–2 M deep, turbid hypersaline	0.043–0.066	2
North Sea Fladen Ground, May bloom (Steele, 1956)	0.10	1.7
Wesslingsee, Bavaria, 10 M deep (Gessner, 1949)	0.9	....
Pool, 30 cm. deep (Gessner, 1949)	1.3	....
Lake Suwa, Japan, M deep (Ichimura, 1954)		
Summer	0.2	1.4
Winter	0.006	6.3
Wisconsin Lakes, M deep (Manning and Juday, 1941)	0.05–1.0	0.8–3.6
Dinoflagellate bloom, New Haven Conn. marine (Conover, 1954)	0.10	1.7
Lunzer Untersee (Gessner, 1949)	0.60	....
Lake Washington, Washington (Edmondson, Anderson and Peterson, 1956)	0.015–0.075	5
Diatom bloom, Moriches bay, 1 M (Ryther et al., 1958)	0.20	4.5
Sewage Pond, Kadoka, S. D. (Bartsch and Allum, 1957) euphotic zone 20 cm.	1.5	2
Corpus Christi Bay, Texas, depth 4 m. August 9 and 22, 1957	0.036–0.200	....
Marine pool, stagnant, filled from flood tide, Port Aransas, Texas, Aug. 6, 1957, 1 m. deep	0.356	....
Gulf, Port Aransas, Texas, 30 M deep, January, 1958	0.18	....
REEF MATERIALS AND CALCAREOUS ALGAE		
Coral Reef, Eniwetok (Odum and Odum, 1955)		
Whole Reef	0.5	4.0
Anemone sheet, *Zoanthus pulchelus*, Lajas, Puerto Rico	0.92	....
Reef corals and calcareous algae, Lajas, Puerto Rico		
Montastrea sp.	0.31	....
Porites asteroides	1.54	....
Dendrogyra cylindricus	1.35	....
Diploria clivosa	0.98	....
Penicillus capitatus ball, from center	1.72	....
Halimeda opuntia clump	2.75	....
ALGAL CULTURES		
Chlorella film, dense (Myers, 1954) Chlorophyll estimated from biomass	0.5	3.0
Sewage culture (Ludwig, et al, 1951)	....	2.0
Dunaliella culture (Ryther 1956a)	....	1–6
LITTORAL AND EMERGENT PLANT COMMUNITIES		
Water Hyacinth, Guadalupe River, Route 35, Texas, *Eichornia*, June 23, 1958	1.38 (1.20, 1.72)	....
Attached Algae on the Jetty at Port Aransas, Texas,		
Gelidium sp., *Ulva fasciola*, and *Cladophora fasciculus*	0.66–0.91	....
Centroceras clavulatum	0.09–0.24	....
Encrustations	0.72	....
Spartina sp., Port Aransas, Texas, March 4, 1958	0.105–0.27	....
Algal scum on intertidal mud, Port Aransas, Texas	0.215	....
Salicornia sp., Laguna Madre, Texas, August, 1957	0.054–0.20	....
Rocky shore intertidal seaweeds Woods Hole, Mass. (E. P. Odum and Gifford, personal communication)	0.5–1.5	....
Red Mangrove Swamp, *Rhizopora*, Lajas, Puerto Rico	0.38	0.42
Black Mangrove Swamp, *Avicennia*, Lajas, Puerto Rico	0.48	0.45
Sand in the surf zone, Port Aransas, Texas	0.00	....
Cattail Marsh, July 22, 1957, Aransas Pass, Texas	0.94	....

Chlorophyll a

SHALLOW AQUATIC COMMUNIT
(plankton minor)
Silver Springs, freshwater eelgra
Turtle Grass, Lajas, Puerto Rico
Laguna Madre, Texas, Diplanthe
Redfish Bay, Port Aransas, Texas,
Winter
Thalassia
Diplanthera
Lorentia
Upper ooze algae
Encrusted wood
Summer Mean of 3, July 7–
Blue green algal mat, 0.1 M deep,
Laguna Madre, Texas, Janua
Blue green algal mat, 2 cm. deep,
trough, Beaufort, N. C., Aug
Blue green algal mat, temporary
Texas, 0.1 M deep, May 26, 1
Minter Spring, Brazos Co., Texas,
brick walls (Abbott and Ho
Algal ooze on sand, Laguna Mad
Rocky mountain stream, Utah,
Algae on live oyster reef, 1 M dee
Bay, Texas
Blue-green algal mat in flowing
and Hoskin, 1957)
Aufwuchs on glass slides, Silver
Blue-green algal mat, polluted str
Refugio, Texas, Aug. 9, 195
TERRESTRIAL COMMUNITIES
Northern Europe
Beech Forest (Gessner, 194
Birch Forest (Gessner, 1949
Meadow, *Dactylis glomerata,*
(Gessner, 1949)
Lower Montane Rainforest, Puer
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Domestic Red Clover, Port Aran
Sugar Cane, Mature, Lajas, Puer
(Net)
Dune Grass, Port Aransas, Tex
Live Oak, Aransas Pass, Texas,
Opuntia sp., after rains, Aransas
computed per area of cactu
Opuntia dilleni, Lajas, Puerto R
computed per area of cactu
Mesquite thicket, Aransas Pass,
Desert herbs, Agua Dulce, Texa
Old field, mixed plants, July 22,
Pasture grasses, Welder Wildlife
July 25, 1957

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[a] New assimilation numbers of land commu
W. Abbott from a system in use by Dr. L. P
metabolism of aquatic communities are meas
and Park, Hood, and Odum, 1958).

TABLE 2—Continued

Chlorophyll and Assimilation Number in Communities

	Euphotic Zone Chlorophyll "A" Gm./M.^{2}	Assimilation[a] Number Oxygen gm./gm./hr.
SHALLOW AQUATIC COMMUNITIES WITH BOTTOM PLANTS (plankton minor)		
Silver Springs, freshwater eelgrass, *Sagittaria*, 1.7 M deep	3.0	0.5
Turtle Grass, Lajas, Puerto Rico, *Thalassia*, 1 M deep	0.43	....
Laguna Madre, Texas, Diplanthera, 1 M deep	0.041–0.30	0.5–1.5
Redfish Bay, Port Aransas, Texas, benthic plants 0.5 M deep:		
Winter		
Thalassia	0.06–0.48	....
Diplanthera	0.08–0.15	....
Lorentia	0.007	....
Upper ooze algae	0.09–0.23	....
Encrusted wood	0.067	....
Summer Mean of 3, July 7–8, 1957	1.0	2.0
Blue green algal mat, 0.1 M deep, salt flats of Laguna Madre, Texas, January, 1957	0.28–0.38	....
Blue green algal mat, 2 cm. deep, artesian water trough, Beaufort, N. C., August, 1956	0.66	....
Blue green algal mat, temporary salt pond, Portland, Texas, 0.1 M deep, May 26, 1958	0.55	0.02
	(0.38–0.75)	....
Minter Spring, Brazos Co., Texas, pH 5.8 algae on brick walls (Abbott and Hoese)	0.45	....
Algal ooze on sand, Laguna Madre, Texas, January,	0.32–0.60	....
Rocky mountain stream, Utah, McConnell (1958)	0.3–1.6	0.7–2.0
Algae on live oyster reef, 1 M deep, turbid, Galveston Bay, Texas	0.32–0.41	....
Blue-green algal mat in flowing microcosm (Odum and Hoskin, 1957)	0.03–0.38	0.7–2.1
Aufwuchs on glass slides, Silver Springs (Yount, 1956)	0.5–1.5	....
Blue-green algal mat, polluted stream, Mission River, Refugio, Texas, Aug. 9, 1957	2.5	....
TERRESTRIAL COMMUNITIES		
Northern Europe		
Beech Forest (Gessner, 1949)	1.3	....
Birch Forest (Gessner, 1949)	0.9	....
Meadow, *Dactylis glomerata*, *Galium molugo* (Gessner, 1949)	1.0	....
Lower Montane Rainforest, Puerto Rico (Odum, Abbott, and Selander, unpublished data)	3.0	4
Domestic Red Clover, Port Aransas, Texas, March 5, 1958	0.59–0.81	....
Sugar Cane, Mature, Lajas, Puerto Rico, January, 1958 (Net)	2.5	0.5
Dune Grass, Port Aransas, Texas, July, 1957	0.1–0.8	....
Live Oak, Aransas Pass, Texas, July, 1957	0.51–1.68	....
Opuntia sp., after rains, Aransas Pass, Texas, July, 1957, computed per area of cactus patch	4.0	....
Opuntia dilleni, Lajas, Puerto Rico, dry season, computed per area of cactus patch	0.78	....
Mesquite thicket, Aransas Pass, Texas, July, 1957	0.74–1.1	....
Desert herbs, Agua Dulce, Texas, August 1, 1957	0.16–0.085	....
Old field, mixed plants, July 22, 1957, Aransas Pass, Texas	0.032	....
Pasture grasses, Welder Wildlife Refuge, Sinton, Texas, July 25, 1957	0.31–0.89	....

[a] New assimilation numbers of land communities reported here were made with a modified CO_2 absorption train adapted by Abbott from a system in use by Dr. L. Pomeroy of the University of Georgia Marine Institute. Measurements of community etabolism of aquatic communities are measured with diurnal curves, bottle methods and bell jars (Odum and Hoskins, 1958; d Park, Hood, and Odum, 1958).

Table 3

Comparison of Chlorophyll and Assimilation Number in Benthic Plants and Phytoplankton in Laguna Madre of Texas

	Chlorophyll "A" Gm./M.^{2}	Assimilation Number Oxygen gm./gm./hr.
WINTER, 1957		
Plankton	0.002–0.043	2.7–4.5[b]
Benthos:		
Diplanthera wrightii	0.012–0.019	....
Bottom ooze, upper 1 cm.	0.029–0.071	
Total Benthos	0.041–0.090	0.75–1.5[c]
SUMMER, 1957 (August)		
Plankton	0.031	....
Benthos:		
Diplanthera wrightii	0.08–0.28	....
Bottom ooze, upper 1 cm.	0.094	....
Total Benthos	0.27	1.5[a]
FALL, 1957		
Benthos:		
Diplanthera wrightii	0.018–0.16	....
Bottom ooze, upper 1 cm.	0.010–0.013	....
Total Benthos	0.090–0.17	....
SPRING, 1958		
Plankton	0.002	3.8[b]
Benthos:		
Diplanthera wrightii	0.041–0.180	....
Bottom ooze, upper 1 cm.	0.106–0.120	...
Total Benthos	0.15–0.30	0.5–0.9[c]

[a] Diurnal curve method.
[b] Light and dark bottle method.
[c] Light and dark bell jars.

in their systems of chlorophyll control means for keeping the chlorophyll at a low concentration until the time at which it normally becomes effective.

It is also possible that some plants are adapted to exist indefinitely with a mixture of heterotrophic and photosynthetic energy sources. Myers and Graham (1956) suggest such plants may develop less chlorophyll for the same light intensity than if photosynthesis were the only energy source. Some such explanation may account for the low concentrations of chlorophyll per leaf or cell in bromeliads in the rain forest (unpublished data), *Ochromonas* studied by Myers, and Graham (1956), some shade leaves on the lower parts of trees, some herbaceous ferns, and some plankton.

In communities it is possible that chlorophyll of heterotrophs may serve as a concealing agent or a means to shade out competitors. For example leaves may be maintained on trees even below compensation point thus removing light that might be used by efficient ground competitors for soil nutrients.

Chlorophyll in Communities

As described in the preceding review and theoretical section, the chlorophyll of whole communities is a function of the several mechanisms and environmental factors. The interplay of the various factors produces varied patterns in vertical chlorophyll structure, in temporal sequence, and in the extremely diverse situations where life exists. In the following paragraphs brief mention is made of some patterns that result when environmental factors affect the chlorophyll adaptation mechanisms in nature.

Comparative Chlorophyll Data from Diverse Communities

In Table 2 are gathered Chlorophyll "A" data for the whole euphotic zone of various kinds of communities. Although more divergent than Gessner's first report (1949) indicated, the data are similar in order of magnitude. In seasons with maximum light intensity the Chlorophyll "A" ranges from about 0.1 gm./M^2 to 3.0 gm./M^2. Lower values are found in seasons with less light and in environments limited by extreme environmental factors.

The general green appearance of terrestrial communities is reflected in high Chlorophyll "A" values. Where clear waters are present so that high light intensities can reach aquatic plants, chlorophyll values in the water may approach those on land. For example, reef substrates, shallow and fertile algal blooms, Silver Springs, and aufwuchs may develop 1 to 3 gm./M^2 Chlorophyll "A".

Correlations of Chlorophyll "A" with conditions favoring photosynthetic fertility have been confirmed. Low values, for example, have been found in plankton of the sea beach, a cactus patch in a dry regime, winter conditions where cloud covers are heavy, and in bays turbid and shaded by silt. High values were found for such generally productive types as water hyacinths, cattails, intertidal algae on rock jetties, fertilized and shallow stream bottoms, and rain forests.

The general relationship of community chlorophyll and photosynthesis is indicated by the general uniformity of assimilation numbers which range generally 0.4 to 4.0 gm./gm./hr. (Table 2). These community assimilation numbers may be expected to be more conservative than the assimilation numbers of community parts. Whereas the assimilation number of cells varies with age, light adaptation, and nutrients, a community tends to have some of all kinds of physiological states with a less extreme mean.

From the range of data in Table 2 it is concluded that no one assimilation number may be assumed for all communities at every season, but it may be possible to predict assimilation values for a type of community if something of the conditions of light, age, and nutrient abundance is known.

In general plankton communities have somewhat larger assimilation numbers than leafy and thick celled systems. In Laguna Madre (Table 3) where plankton simultaneously share productivity with bottom plants, assimilation numbers for plankton (2 to 4.5 gm./gm./hr.) are higher than the values in the benthos (0.5–1.5 gm./gm./hr.). For terrestrial communities data on assimilation numbers are too few for generalization, although there are as yet no reasons to expect differences.

Vertical Distribution of Chlorophyll in Communities

Several of the factors discussed in the theoretical sections of the paper affect the vertical structure of chlorophyll in the natural community in known ways. Light decreases from the surface downward producing more chlorophyll and lower assimilation numbers with depth. In nature, however, factors other than light are also important. The presence of better nutrient conditions from regeneration at the bottom of a water body tends to increase assimilation numbers there. The stratification of aquatic herbivores in the shade during the day tends to decrease chlorophyll at the bottom by herbivore grazing. For example, Anderson (1958) showed the role of grazing in limiting chlorophyll in experimental lake studies. In some eutrophic lakes with shallow clear epilimnions the euphotic zone may be in the hypolimnion with favorable conditions for accumulation of sinking, non-functional chlorophyll. The oxygen content of the hypolimnion thus can affect the chlorophyll by limiting the herbivore populations. In stratified situations, high temperature at the top may increase assimilation numbers there. The turbulence may control the size of plant cells that may be suspended, Riley, Stommel, and Bumpus (1949). With more turbulence, larger cells are possible with more chlorophyll per community area, less chlorophyll per gram, and lower assimilation numbers. Vertical layering of species is well known. See Talling (1957) for a recent example and discussion of the stratification of phytoplankton populations. Unless there are motile or floating species, cells fall away from the very topmost surface even in very turbulent conditions.

Whereas the top of a stratified community adapted to high light intensity may have high assimilation numbers (Ichimura, 1956) and less chlorophyll per cell, other communities like those in the mixing epilimnetic waters of lakes and seas may have cells adapted to an average position in their daily rises and falls. Uniform concentrations of chlorophyll with depth often occur especially during times of vertical mixing (Manning and Juday, 1941; Ichimura and Siajo, 1958). Such cells may not be genetically capable of adaptation to the highest steady light intensity to the extent of species adapted remain at the top of stratified communities.

Dinoflagellates and other species are known to move vertically concentrating sometimes at the surface and sometimes at deeper levels. In shallow pools some algae may coat the surface with such density that the euphotic zone is only centimeters thick. Pomeroy, Hakin and Ragotzkie (1956) found much of chlorophyll in topmost layers in some dinoflagellate blooms. Bartsch and Allum (1957) found decreasing chlorophyll with depth in stratified sewage pond with a euphotic zone of 20 cm.

All of the varying factors may tend to produce many different patterns of vertical chlorophyll structure. Kozminski (1938) reported 4 types of vertical patterns in Wisconsin lakes. Riley (1940) found all four types in Linsley pond at different times, and Jenkins (1955) found all types in the English channel at different times. Hogetsu and Ichimura (1954) described lakes with chlorophyll increasing with depth in lakes whereas Kozminski (1938) and Manning and Juday (1941) found many waters with chlorophyll increasing with depth. The relative roles of light, grazing and other factors may be reflected in these differences.

The above authors describe many cases with maximum chlorophyll at an intermediate depth in the euphotic zone in lakes and seas especially, Riley, Stommel, and Bumpus (1949). A similar pattern exists in "grass" beds of Silver Springs (Odum, 1957). In a red mangrove swamp *(Rhizopora)* in La Parquerra, Lajas, Puerto Rico, the vertical distribution of Chlorophyll "A" in gm./M^2. of leaf contained a maximum at an intermediate level as follows:

above ground	gm./M^2
6M.	0.25
5M.	0.19
4M.	0.32
3M.	0.35
2M.	0.23
1M.	0.25

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The reef structures in the windward reef at Eniwetok are within a meter of the surface in water of almost maximum clarity so that light penetration into the reef is likely to be maximal. As described previously (Odum and Odum, 1955), intense green bands of boring algae grow in all the substrates including the live corals. Elsewhere in Hawaii, Key West Florida, and La Parguerra, Puerto Rico, these authors have since had an opportunity to break open coral heads for comparison. Although some green bands exist, in general the intense banding observed in Eniwetok has not been observed. It seems likely that the greater depth and greater turbidity intercepts more of the incident light in the other areas examined. Thus less light penetrates into the limestone to support deep-subsurface algal growth. The deep algal bands in reef materials are clearly in shade and are likely to have more chlorophyll per cell and a low assimilation number relative to the more brightly illuminated zooxanthellae which are in a zone of light adaptation.

With so many kinds of vertical chlorophyll patterns it is not possible to assume vertical chlorophyll structure or to consider as representative chlorophyll measurements per volume from only part of the euphotic column. It remains for further work to determine if the various vertical chlorophyll patterns are in each case self adapted for maximum community photosynthesis under the circumstances as postulated in the previous sections.

SEASONAL CHANGES OF CHLOROPHYLL IN COMMUNITIES

The chlorophyll in the euphotic zone of a community in the course of a year is subject to changes in many of the aforementioned controlling factors, nutrients, temperature, turbulence, and grazing by herbivores. Thus with different annual factor sequences in different areas, annual patterns of chlorophyll differ also. The chlorophyll of the whole euphotic zone increases with light, with nutrients, when graizng diminishes, and with conditions leading to retarded chemical turnover in the cells. The area-based assimilation number for the whole euphotic zone increases with light, nutrients, temperature, and conditions favoring high turnover rates.

Many annual curves for chlorophyll and assimilation number have been reported; there is no generalized pattern. Riley, Stommel, and Bumpus (1949), Atkins and Jenkins (1953), and Conover (1954), for example, frequently found maximum chlorophyll and assimilation number in the spring since conditions of increasing light, low grazing, and maximal nutrients often occurred together. Gessner (1944) found low assimilation numbers in winter. Further south Margalef, Munoz and Herrera (1957) found more plant pigments on the Spanish coast in winter. In 3 Japanese lakes Hogetsu and Ichimura (1954) and Ichimura (1956) found that maximum chlorophyll of the whole euphotic zone was in the summer. Much non-functional chlorophyll was found sinking into the dark hypolimnion. Anderson (1958) found high chlorophyll values in spring and early fall in saline Lake Lenore, but in Soap Lake chlorophyll was minimal in Fall. In the present study seasonal comparisons in the Laguna Madre of Texas (Table 3) indicate lower chlorophyll contents, lower production, and higher assimilation numbers in the winter season. N. Marshall (1955) found as much variation in Alligator Harbor, Florida from day to day as seasonally. In these varied sequences there is neither proof nor disproof for theories of chlorophyll adaptability but increasing knowledge of seasonal patterns advances the science of comparative ecology and may permit more accurate use of chlorophyll and assimilation number for measurement of primary photosynthesis.

Chlorophyll, Community Age, and Succession

Although a number of authors have studied the time sequence of chlorophyll and photosynthesis of single plants and algal cultures as age studies, it is difficult to separate the effects of physiological age from such community properties as diminishing nutrients and self-shading.

If with old age a machine decreases the effectiveness of its energy transfers with more energy lost to leakages, more input energy may be required for the same work output. In the cannon-ball catcher machine analogy more cups may be needed as the machine ages in order to accomplish the same job. Whether the increase of chlorophyll with age of cells has any similarity of basis with senescence of the cannonball catcher is unknown.

The increase in chlorophyll in an aging culture or plant is related to the increased self shading. Cells from older plants and cultures are larger with less turnover, more chlorophyll, and lower assimilation numbers (Willstatter and Stoll, 1918; Ludwig, Ostwald, Gotaas, and Lynch, 1951). Margalef (1957) found more chlorophyll, larger size, and lower turnover in older cells of *Scenedesmus obliquus*. Self respiration rate is higher so that self nutrient regeneration is greater. Thus several factors affect chlorophyll simultaneously in an aging plant or culture. Individual Chlorella cells growing in synchronous culture developed maximum photosynthesis 3–4 hours after division (Sorokin, 1957). Whether a community has age other than the age of its individuals has yet to be determined. At present community time sequences are termed succession.

In plant succession in nature, early colonization is followed first by increases in community chlorophyll, bright conditions, and high assimilation numbers. Later these may decline. There is no certainty whether the last and most stable stages of succession have as much chlorophyll and assimilation as intermediate stages. A flowing microcosm (Odum and Hoskin, 1957) had maximum chlorophyll and assimilation during favorable nutrient conditions of succession. The spring blooms in north temperature waters are accompanied by excessive chlorophyll and assimilation followed by later stages with lower values. Very high chlorophyll contents have also been found in climax rainforests and coral reefs.

Thus as yet there is no proved single sequence of chlorophyll and assimilation number in succession. It is likely that communities can be grouped according to productivity sequences for predictive purposes.

Diurnal Changes in Chlorophyll

It may be postulated that the adaptive mechanisms suggested above as the cause of the temporal variation in chlorophyll also operate in daily cycles. Diurnal variations in exported chlorophyll with midday maximum were measured in Silver Springs (Odum, 1957). Diurnal variation of plankton chlorophyll has been shown in several environments. Mr. Ray S. Wheeler (unpublished student report, Duke University, 1956) in an estuarine lagoon near Beaufort, N. C. found a diurnal range 6 to 26 mg. chlorophyll per M^3 with maximum amounts in the afternoon. Yentsch and Ryther (1957) and Shimada (1958) found a maximum chlorophyll per volume of water at dawn in marine waters although the daily variation in chlorophyll of the total euphotic column was not measured. Ten measurements in Copano Bay, near Port Aransas, Texas showed a wide range (0–25 mg./M^3) Mitrakos, Bünning, and Ebshadt (1957) found a 10 per cent diurnal variation in chlorophyll content of leaves of a land plant, *Perilla ocymoides* with more chlorophyll in the middle of the day.

A diurnal variation in assimilation number was found in Lake Teganuma by Ichimura (1958) with a noon maximum.

It is not difficult hypothetically to interpret the diurnal maxima in terms of adjustments of chlorophyll to maintain optimum output drive. For example, early morning chlorophyll maxima in a cell may be attributed to the need for more chlorophyll per cell at low light intensity. Nutrient depletion and temperature rise late in the day may prevent the rise of the chlorophyll in the evening.

Area-Based Procedure for Determining Community Photosynthesis From Chlorophyll

There have been a number of attempts to measure photosynthetic rate from chlorophyll measurements as a field method in aquatic ecology (Riley, 1940; Manning and Juday, 1941; Edmondsen and Edmondsen, 1947; Hogetsu and Ichimura, 1954; Edmondsen, 1955; Ryther, 1956b; Ryther and Yentsch, 1957, 1958; Holmes, Shaefer, and Shimada, 1957 and others). These studies have dealt with plankton communities and have been based on chlorophyll concentrations per volume. For example, Ryther and Yentsch in work in the North Atlantic and coastal waters of the northeastern United States measure the chlorophyll concentration, the extinction coefficient of light in the euphotic zone, an assumed assimilation number based on previous photosynthetic measurements in similar environments, and an assumed vertical distribution of assimilation numbers. As indicated by data in Table 2, such methods are not general since assimilation number varies. Even in plankton communities there is no reason to expect assimilation numbers to be constant. Holmes, Shaefer, and Shimada (1957) were unable to confirm the chlorophyll procedure as used by Ryther and Yentsch for other areas. Such methods which involve knowledge or assumptions of structure are not readily adapted to diverse communities on land, reefs, and shallow bays where the euphotic zone may be variable or concentrated in a thin layer.

In order to make the chlorophyll method more general it is suggested that chlorophyll and assimilation numbers be measured for the whole euphotic zone per area as in Table 2. For each type of community measurements should be made at all seasons, light, and nutrient regimes, so that a group of assimilation numbers become available. Thereafter, it will be possible for photosynthesis to be related to chlorophyll with more certainty.

For example, data summarized in Table 3 for the upper Laguna Madre of Texas can be used there in subsequent years with occasional checks to provide rapid estimates of the primary production from the relatively rapid survey of chlorophyll. The chlorophyll methods previously used by aquatic ecologists can thus be adapted for community work on land as suggested by the preliminary measurements in this paper. Even where no measurements of assimilation number are made, it may be possible to develop approximate data on community photosynthesis of land areas by use of assimilation numbers of somewhat similar community systems. The role of important land factors such as water in controlling production in arid areas may be followed with community chlorophyll assay.

Under natural conditions the period of insolation from which the assimilation number is computed should be considered. Ideally the period of measurement should be the entire day and the results presented as grams of oxygen per gram of chlorophyll per *average* hour of insolation. An exact half of a solar day seems to be the next most favorable period although there is no evidence to indicate that symmetry of photosynthetic activity may be assumed for half days.

Summary

1. Measurements of Chlorophyll "A" and assimilation number have been made in widely contrasting types of communities in order to permit generalization about distribution and role of chlorophyll in ecology on land as well as in water. The chlorophyll of whole euphotic zones in well lighted seasons generally ranges from 0.1 to 3.0 gm./M². The assimilation number of such whole communities generally ranges from 0.4 to 40 gm. 0_2/gm. Chlorophyll "A"/hr.

2. The cannon-ball catcher analogy is utilized to explain some known adjustments of chlorophyll. Chlorophyll "A" systems are believed self adjustable for maintaining optimum input-output power ratios. Changing the numbers of cups of the cannon-ball catcher machine is energetically equivalent to changing the amount of chlorophyll. The role of the ecological community in controlling the system of chlorophyll in nature is postulated. The difference between adaptation of single plants and the adaptation of the whole community is emphasized.

3. Measurments with both the Beckman DU spectrophotometer and the Bausch and Lomb spectrophotometer have been made in order to adapt the chlorophyll method of Richards and Thompson (1952) to general ecological use. The abbreviated equation for chlorophyll when extracted with 90 per cent acetone and measured with a narrow band pass spectrophotometer is: Chlorophyll "A" in mg./l = 13.4 (optical density at 665 millimicrons with 1 cm. light path). Measurements with a broad band pass instrument require slightly different conversion factors depending on the types of plants.

4. Measurements are reported indicating the impracticality of separating functional and non-functional chlorophyll. The convention of including all euphotic zone chlorophyll is suggested.

5. Errors in chlorophyll assay due to extraction procedures, solvent variation, and assumptions in the Richards and Thompson procedure are discussed. Errors are in general less than those due to sampling error and the great variability of natural chlorophyll distribution.

6. Communities are classified in four types with respect to light intensity-chlorophyll adjustments: (1) stratified communities with levels of light-shade adaptation. (2) shaded communities. (3) mixing communities with plant cells exposed to fluctuating light intensity. (4) bright thin communities without shade adapted parts. Total chlorophyll and total community photosynthesis is maximal in stratified type (1–60 gm./M²/day). Assimilation number is maximal in the thin bright type (8 to 40 gm. oxygen/gm. Chlorophyll "A"/hour). Efficiency is greatest in the shaded community type (10 to 30%).

7. Total photosynthesis and chlorophyll of whole euphotic zones (unlike the photosynthesis and chlorophyll of community parts) increases with light intensity without a maximum even at full sunlight. These are exceptions.

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Bartsch, A. F. and M. O.
ponds. Limnol. and Oc
Brugger, J. E. 1957. Fluo
pp. 113–117 *in* Gaffro
Burlew, J. S. 1953. Algal
Conover, S. M. 1954. Obs
J. Mar. Res., 13: 145–
———. 1956. Ocean
Coll., 15: 62–112.
Creitz, G. I. and F. A. Ri
pigment analysis. II
plankton pigments. J
Deevey, E. S. 1940. Lim
Amer. J. Sci., 338: 7
Duxbury, A. C. and C.
Edmondson, W. T. 195
(supplement): 451
———. 1956. The
161–174.
Edmondson, W. T., G.
Washington. Limn
Edmondson, W. T. an
J. Mar. Res., 6: 22
Franck, James, and W
Press, pp. 1–500.
Gessner, F. 1944. Der
(Plankt.), 40, 68

8. Cannon-ball catcher theory is presented to account for the low concentrations of community chlorophyll with limiting nutrients, with high temperatures, with small plant size, with heterotrophy, and in water as contrasted with land.

9. Data on the annual and vertical patterns of chlorophyll are reviewed in terms of the factors controlling community chlorophyll adaptation. There are no universal patterns for maxima and minima, but characteristic types exist for particular kinds of communities.

10. For greatest comparative value and least variability, measurements of chlorophyll for the purpose of estimating photosynthesis should be made for the whole euphotic zone on an area of community basis. Photosynthetic measurement procedures based on single assimilation numbers do not have general applicability. For maximum accuracy community assimilation numbers must be determined for each characteristic environment, condition, and season.

Rough community photosynthesis values may be obtained in unknown communities by selection of assimilation numbers reported for similar community types from data like that in Table 2. With adequate caution the abbreviated chlorophyll method may be used widely over the communities of the earth to obtain production estimates where direct measurements are prohibitive in cost.

LITERATURE CITED

Aleem, A. A. 1950. The diatom community inhabiting the mudflats at Whitstable. New Phytol., 49: 174–188.

Anderson, G. C. 1958. Seasonal characteristics of two saline lakes in Washington. Limnol. and Oceanogr., 3: 51–68.

Atkins, W. R. G. and P. Jenkins. 1953. Seasonal changes in the phytoplankton during the year 1951–52 as indicated by spectrophotometric chlorophyll estimations. J. Mar. biol. Assn. U. K., 31: 495–507.

Bartsch, A. F. and M. O. Allum. 1957. Biological factors in the treatment of raw sewage in artificial ponds. Limnol. and Oceanogr., 2: 77–84.

Brugger, J. E. 1957. Fluorescence yield of chlorophyll in Chlorella as a function of light intensity. pp. 113–117 *in* Gaffron, H. et al. Research in Photosynthesis, N. Y., Interscience, pp. 1–524.

Burlew, J. S. 1953. Algal culture from laboratory to pilot plant. Publ. Carneg. Instn., 600: 1–357.

Conover, S. M. 1954. Observations on the structure of red tides in New Haven Harbor, Connecticut. J. Mar. Res., 13: 145–155.

———. 1956. Oceanography of Long Island Sound. IV. Phytoplankton. Bull. Bing. oceanogr. Coll., 15: 62–112.

Creitz, G. I. and F. A. Richards. 1955. The estimation and characterization of plankton populations by pigment analysis. III. A note on the use of "millipore" membrane filters in the estimation of plankton pigments. J. Mar. Res., 14: 211–225.

Deevey, E. S. 1940. Limnological Studies in Connecticut. V. A contribution to regional limnology. Amer. J. Sci., 338: 717–741.

Duxbury, A. C. and C. S. Yentsch. 1956. Plankton pigment nomographs. J. Mar. Res., 15: 92–101.

Edmondson, W. T. 1955. Factors affecting productivity in fertilized sea water. Deep Sea Res., 3 (supplement): 451–464.

———. 1956. The relation of photosynthesis by phytoplankton to light in lakes. Ecology, 37: 161–174.

Edmondson, W. T., G. C. Anderson, and D. R. Peterson. 1956. Artificial eutrophication of Lake Washington. Limnol. and Oceanogr., 1: 47–53.

Edmondson, W. T. and Y. H. Edmondson. 1947. Measurement of production in fertilized salt water. J. Mar. Res., 6: 228–246.

Franck, James, and Walter E. Loomis, Ed., 1950. Photosynthesis in Plants. Ames, Iowa State College Press, pp. 1–500.

Gessner, F. 1944. Der chlorophyllgehalt der Seen als Ausdruck ihrer Productivitat. Arch. Hydrobiol. (Plankt.), 40, 686.

——————. 1949. Der Chlorophyllgehalt in See und seine photosynthetische Valenz als physikalisches Problem. Schweiz. Z. Hydrol., 11: 378–410.

——————. 1955. Hydrobotanik. Bd. I. Energiehaushalt. Berlin, Verlag der Wissenschaften, pp.

Gillbricht, M. 1951. Untersuchungen zur Productions biologie des Planktons in der Kieler Bu Kieler Meeresforsch., 8: 173–191.

Harvey, H. W. 1934. Measurement of phytoplankton population. J. Mar. biol. Assoc. U. K., 19 773.

——————. 1955. Chemistry and Fertility of Sea Water. England, Cambridge, 225 pp.

Hill, Robert, and C. P. Whittingham. 1955. *Photosynthesis*. London, Methuen & Co. Ltd., pp.

Hogetsu, K. and S. Ichimura. 1954. Studies on the biological production of Lake Suwa. VI. ecological studies on the production of phytoplankton. Jap. J. Bot., 14(2): 280–303.

Holmes, R. W., M. B. Schaefer and B. M. Shimada. 1957. Primary production, chlorophyll, zooplankton volumes in the tropical eastern Pacific Ocean. Bull. Inter. Amer. Tropical Comm., 2: 121–169.

Ichimura, Shun-ei. 1954. Ecological studies on the plankton in paddy fields. I. Seasonal fluctua in the standing crop and productivity of plankton. Jap. J. Bot., 14(2): 269–279.

——————. 1956. On the standing crop and productive structure of phytoplankton communit some laes of Central Japan. Bot. Mag., Tokyo, 69(811): 7–16.

——————. 1958. On the photosynthesis of natural phytoplankton under Field Conditions. Bot. M Tokyo, 71(837): 110–116.

—————— and Y. Saijo. 1958. On the application of 14C-method to measuring organic matter duction in the lake. Bot. Map., Tokyo, 71 (839): 174–180.

Jenkin, P. M. 1937. Oxygen production by the diatom *Cascinodiscus excentricus* Ehr. in relation submarine illumination in the English Channel. J. Mar. biol. Assoc. U. K., 22: 301–343.

Jenkins, P. 1955. Changes in phytoplankton as indicated by spectrophotometric chlorophyll estimati Deep Sea Res., 3 (Supplement): 58–67.

Katz, E. 1949. Chlorophyll fluorescence as an energy flow meter for photosynthesis. pp. 287–348, Franck and Loomis (1950).

Kozminski, Z. 1938. Amount and distribution of the chlorophyll in some lakes of northeastern W consin. Trans. Wis. Acad. Sci., Arts Lett., 31: 411–438.

Kramer, P. J. 1958. Photosynthesis of trees as affected by their environment. pp. 157–186 *in* Thiman K. V., The Physiology of Forest Trees. N. Y., Ronald Press, pp. 1–678.

Krey, J. 1952. Untersuchungen Zum Sestongehalt des Meerwassers 1: Der Sestongehalt in d westlichen Oostsee und unter Helgoland. Ber. dtsch. Komm. Meeresforsch., 12: 431–456.

Ludwig, H. F., W. J. Oswald, H. B. Gotaas and V. Lynch. 1951. Algae symbiosis in oxidation pond I. Growth Characteristics of *Euglena gracilis* cultures in sewage. Sewage Industr. Wastes Engn 23: 1337–1355.

MacKinney, G. 1941. Absorption of light by chlorophyll solution. J. biol. Chem., 140: 315–322.

Manning, W. M., C. Juday, and M. Wolf. 1938. Photosynthesis of aquatic plants at different depth in Trout Lake, Trans. Wis. Acad. Sci., Arts Lett., 31: 377–410.

——————, and R. E. Juday. 1941. The chlorophyll content and productivity of some lakes in north eastern Wisconsin. Trans. Wis. Acad. Sci., Arts Lett., 33: 363–393.

Margalef, R. 1957. Nuevos aspectas del problema de la suspension en los organismos planctonicos Investigacion Pesquero, 7: 105–116.

Margalef, R., F. Munoz & J. Herrera. 1957. Fitoplancton de las costas de Castellon de eneros de 195 a junio de 1956. Invest. Pesquera, 7: 3–31.

Marshall, N. 1955. Measurements of plankton feeders in relation to gross production. Ecology, 36 360–362.

——————. 1956. Chlorophyll A in the phytoplankton in coastal waters of the eastern Gulf of Mexico J. Mar. Res., 15: 14–32.

Marshall, S. M. and N. P. Orr. 1929. A study of the spring diatom increase in Lake Striven. J. Mar biol. Assn. U. K., 16: ......–......

McConnell, Wm. J. 1958. Chlorophyll and productivity in a mountain river. Ph.D. thesis, Utah State Univ. Library, Logan, Utah.

Mitrakos, D. von, E. Bünning, N. F. Efshadt. 1957. Endogen-Tagesperiodische Schwankungen des Chloroplasten Farbstoffe. Z. Naturf., 126(12): 813–814.

Myers, J. 1954. Basic remarks on the use of plants as biological gas exchangers in a closed system J. Aviation Med., 25: 407–411.

Myers, J. and J. Graham. 1956. The role of photosynthesis in the physiology of Ochromonas. J. cell comp. Physiol., 47: 397–414.

Myers, J. and W. A. Kratz. 1955. Relations between pigment content and photosynthetic characteristics in a blue-green alga. J. gen. Physiol., 39: 11–22.

Nihei, T., T. Sasa, S. Miyachi, K. Suzuki and H. Tamiya. 1954. Change of photosynthesis activity of Chorella cells during the course of their normal life cycle. Arch. Mikrobiol., 21: 155–164.

Odum, E. P., E. J. Kuenzler, and M. X. Blunt. 1958. Uptake of P^{32} and primary productivity in marine benthic algae. Limnol. and Oceanogr., 3: 340–345.

Odum, H. T. 1956. Efficiencies, size of organisms, and community structure. Ecology, 37: 592–597.

———. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecol. Monogr., 27: 55–112.

Odum, H. T., and C. M. Hoskins. 1957. Metabolism at a laboratory stream microcosm. Publ. Inst. Mar. Sci. Univ. Tex., 4(2): 115–133.

———. 1958. Comparative studies on the metabolism of marine water. Publ. Inst. Mar. Sci. Univ. Tex., 5: 16–46.

Odum, H. T. and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr., 25: 291–320.

Odum, H. T. and R. C. Pinkerton. 1955. Times speed regulator, the optimum efficiency for maximum power output in physical and biological systems. Amer. Scient., 43: 331–343.

Orr, W. L. and J. R. Grady. 1957. Determination of chlorophyll derivatives in marine sediments. Deep Sea Res., 4: 263–271.

Park, K., D. Hood, and H. T. Odum. 1958. Diurnal pH variations in Texas bays and its application to primary production. Publ. Inst. Mar. Sci. Univ. Tex., 5: 47–64.

Phillips, J. N. and J. Myers. 1954. Measurement of algal growth under controlled steady-state conditions. Plant Physiol., 29: 148–152: 152–161.

Pomeroy, L. R., H. H. Haskin, and R. A. Ragotzkie. 1956. Observations on dinoflagellate blooms. Limnol. and Oceanogr., 1: 54–60.

Rabinowitch, E. T. Photosynthesis. Interscience. New York,
———. 1945. Vol. I, pp. 1–603.
———. 1951. Vol. II, Pt. 1, pp. 603–1208.
———. 1956. Vol. II, Pt. 2, pp. 1208–2087.

Richards, F. R. 1952. The estimation and characterization of plankton populations by pigment analyses. I. The absorption spectra of some pigments occurring in diatoms, dinoflagellates, and brown algae. J. Mar. Res., 11: 147–155.

———, with T. G. Thompson. 1952. The estimation and characterization of plankton populations by pigment analysis. II. A spectrophotometric method for the estimation of plankton pigments. J. Mar. Res., 11: 156–172.

Riley, G. A. 1940. Limnological studies in Connecticut. Part III. The plankton of Linsley Pond. Ecol. Monog., 10: 279–306.

Riley, G. A. 1956. Oceanography of Long Island Sound, 1953–1954. IX. Production and Utilization of Organic matter. Bull. Bing. oceanogr. Coll., 15: 324–343.

Rodhe, W., R. A. Vollenweider, and A. Nauwerck. 1958. The primary production and standing crop of phytoplankton. pp. 299–322 *in* A. A. Buzzati-Traverso. Perspectives in Marine Biology. Berkeley, Univ. Calif. Press, pp. 1–621.

———, H. Stommel, and Dean F. Bumpus. 1949. Quantitative ecology of the Western North Atlantic. Bull. Bing. oceanogr. Coll., 12(3): 1–169.

Ryther, J. A. 1956a. Photosynthesis in the ocean as a function of light intensity. Limnol. and Oceanogr., 1: 61–70.

———. 1956b. The measurement of primary production. Limnol. and Oceanogr., 1: 72–84.

Ryther, J. H., E. M. Hulbert, and R. F. Vaccaro. 1958. The dynamics of a diatom bloom. Biol. Bull., 115: 257–268.

Ryther, J. H., and C. S. Yentsch 1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. Limnol. and Oceanogr., 2: 281–286.

———. 1958. Primary production of continental shelf waters off New York. Limnol. and Oceanogr., 3: 327–335.

iargent, M. C. 1940. Effect of light intensity on the development of the photosynthetic mechanism. Plant Physiol., 15: 275–290.

himada, B. M. 1958. Diurnal fluctuations in photosynthesis rate and chlorophyll "A" content of phytoplankton from Eastern Pacific waters. Limnol. and Oceanogr., 3: 336–339.

orokin, C. 1957. Changes in photosynthetic activity in the course of cell development in *Chlorella*. Physiol. Plant., 10: 659–666.

teemann, Nielsen, E. 1954. On organic production in the oceans. J. Cons. int. Explor. Mev., 19: 309–328.

———. 1957. The chlorophyll content and the light utilization in communities of plankton alg and terrestrial higher plants. Physiol. Plant., 10: 1009–1021.

Steele, J. 1956. Plant production on the Fladen Ground. J. Mar. biol. Assn. U. K., 35: 1–33.

Strehler, B. L. 1958. Some energy transduction problems in photosynthesis. Chapter 9 *in* Rudnick, D Rhythmic and Synthetic Processes in Growth. Princeton, Princeton University Press, pp. 171–19

Takeda, T. and H. M. Maruta. 1956. The effect of light intensity and spacing on the photosyntheti rate of rice plant in community conditions. Records of Researches, Faculty of Agriculture, Uni Tokyo, 7: 4–5 (abstract).

Tamiya, H., T. Twamura, K. Shibata, E. Huse, and T. Nihei. 1953. Correlation between photosynthesis and light—independent metabolism in the growth of chlorella. Biochem. Biophys. Acta, 12: 23–40.

Talling, J. F. 1957. Diurnal changes of stratification and photosynthesis in some tropical Africa waters. Proc., Royal Soc., B., 147: 57–83.

Vallentyne, J. R. 1955. Sedimentary chlorophyll determination as a paleobotanical method. Canad. J. Bot., 33: 304–313.

Verduin, J. 1956. Primary production in lakes. Limnol. and Oceanogr., 1: 85–91.

Wassink, E. C., B. Kok, and J. L. P. van Oorschot. 1953. The efficiency of light energy conversion in *Chlorella* cultures as compared with higher plants. pp. 55–62. *in* Burlew (1953).

Willstatter, R. and A. Stoll. 1918. Untersuchungen über die Assimilation der Kohlensäure. Berlin, J. Springer, pp. 1–448.

Yount, J. L. 1956. Factors that control species numbers in Silver Springs, Florida. Limnol. and Oceanogr., 1: 286–295.

Zscheile, F. P., C. L. Comar, and G. Mackinney. 1942. Interlaboratory comparison of absorption spectra by the photoelectric spectrophotometric method.—Determinations on chlorophyll and Weigert's solutions. Plant Physiol., 17: 666–670.