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SOME ESTIMATES OF PRIMARY PRODUCTION RATES IN MICHIGAN PONDS

by

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Photosynthetic fixation of solar energy in ponds is carried on by the attached algae (periphyton), the planktonic algae, and by the larger plants growing on the pond bottom (aquatic macrophytes). In the present study we have attempted to: (1) measure independently rates of energy fixation by these three sources; (2) identify environmental factors which favor one source of production over the others; and (3) compare our production estimates with those made in other ecosystems.

It has been demonstrated experimentally that growth of aquatic macrophytes in some way inhibits phytoplankton production (Hasler and Jones, 1949). The mechanism of this inhibition remains obscure. Undoubtedly a variety of factors are involved and the degree of inhibition differs from one ecosystem to another. It has frequently been suggested that aquatic macrophytes compete with plankton algae for nutrient materials (Embody, 1928; Bennett, 1942;

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Wiebe, 1934). However, shading effects (competition for light) have also been mentioned as mechanisms by which the larger aquatic plants suppress plankton blooms (Hasler and Jones, 1949). The position of periphyton algae in such competitive interaction has not been considered.

Methods used in evaluating production of ponds have been chiefly the measurements of the crops produced by the pond such as bottom fauna and fish (Patriarche and Ball, 1949; Meehean, 1936; Hayne and Ball, 1956). In some instances, an index of the size of the plankton crop has been secured by making plankton counts and transparency measurements. Radioactive carbon (C^{14}) has been used to measure primary production in the ocean and in fresh-water lakes (Strickland, 1960). It affords a convenient and reproducible method of measuring production rates in ponds and should find useful application in pond culture, particularly in situations where one wishes to compare the production of one pond with another.

The attached algae have long been recognized as making a major contribution to the primary production of standing water (Young, 1945). However, few attempts have been made to estimate the energy fixed by this segment of the biota. Newcombe (1950) made quantitative measurements of the periphyton that accumulated on glass slides which were suspended in two southern Michigan lakes. His periphyton results tended to confirm his conclusions, based upon plankton and organic matter measurements, that Walnut Lake was more productive than Sodon Lake. Grzenda (1960) and Grzenda and Brehmer (1960) perfected quantitative techniques for studying periphyton. Grzenda showed that the phytopigments extracted from artificial substrates can be used to estimate the production of organic matter. It is appropriate that the C^{14} method and quantitative periphyton techniques be used to attack the general problem of the interrelationship between the production rates of periphyton, phytoplankton and aquatic macrophytes.

Methods and materials

Four ponds at Michigan State University Agricultural Experiment Station at Lake City, Michigan, were studied between June 15 and September 15, 1960. Routine chemical and physical measurements were made throughout this period. A continuous record of water temperature for the period was obtained from a Taylor thermograph. Hydrogen-ion concentration was determined with a Beckman pH meter (model H). Total alkalinity was measured by titrating samples with 0.02 N H_2SO_4, using methyl-orange as an indicator (Ellis, Westfall and Ellis, 1948). Dissolved oxygen was determined by the unmodified Winkler method. Total phosphorus was measured throughout the summer using a modification of the procedure given by Ellis, Westfall and Ellis (1948). Total iron was determined using the tripyridyl method (American Public Health Association et al., 1955).

The accrual of periphyton on plexiglass plates yields an estimate of net primary production (Grzenda and Brehmer, 1960). Periphyton was scraped from plates with a glass microscope slide and the phytopigment was extracted with 95 percent alcohol. The ash-free dry weight of each periphyton sample was determined by evaporating the solvent and igniting the oven-dry samples in a muffle furnace at 520° C. Samples were weighed before and after ignition on an analytical balance. An estimate of ash-free dry weight of organic matter was obtained by subtracting the weight of ash from the dry weight.

The second source of primary production studied was the aquatic macrophytes. Thirty randomly selected samples of vegetation were obtained from each pond. Each sample consisted of all the plants within a one square-foot plot. All parts of the plants including roots and rhizoids were collected. Samples were drained a constant period of time and then weighed. This weight was recorded as wet weight. The last ten samples collected in each pond were taken to the laboratory for determination of dry weight. They were placed in an oven, dried at 55° C. and weighed. This weight was recorded as dry weight.

The third source of primary production studied was that from planktonic algae. The C^{14} technique as described by Steeman Nielsen (1951, 1952) and the oxygen method were both used to measure this source but the latter technique was abandoned when it was clear that results were not reproducible. Water samples were collected in a plastic container. Samples were introduced into glass-stoppered pyrex bottles which were suspended in the ponds at the depth at which the sample was collected. A series of three bottles was suspended at each depth. Two of the bottles were of clear glass and the third bottle was opaque. Bottles were suspended in each pond at depths of 16 and 32 inches. Before the bottles were suspended, two microcuries of C^{14}, in the form of sodium carbonate, were added with a hypodermic syringe to each bottle. Bottles were exposed for a period of six hours, which began shortly after 9:00 AM. At termination of the 6-hour exposure,bottles were removed from the pond and a 25 ml. subsample from each bottle was filtered through a type HA, millipore filter pad. The pad was allowed to dry and was then cemented to a planchet. The planchet and attached filter pad were then placed in radiological counting equipment and counts of radioactive carbon were obtained. These counts were converted to total assimilated carbon using the formulae given by Steeman Nielsen (1952b). Results were expressed as milligrams of carbon fixed per cubic meter per hour.

Chelated iron (NaFeEEDTA) was introduced into ponds B and C on July 15. The theoretical concentration of chelated iron in ponds B and C, after complete mixing, was one part per million. Diammonium phosphate was added to ponds C and D at a rate of 20 pounds per acre. The theoretical concentration of phosphorus after this treatment was 0.48 mg./1. for pond C and 0.41 mg./1. for pond D. Fertilizer and chelate were applied with a hand operated garden sprayer. These materials were spread as evenly as possible over the entire surface of the ponds.

Between June 16 and June 18, the ponds were drained. The ponds were not refilled until June 24. This period, during which the ponds lay fallow, was of sufficient duration to desiccate and kill the aquatic macrophytes.

Physical and chemical

The general trend of the water temperature followed the temperature of the atmosphere very closely. The water warmed slowly until July 12 when we recorded a maximum of 84° F. Thereafter the ponds cooled gradually until September 8, when a sharp decline in water temperature was observed.

During the study period methyl-orange alkalinity varied between 46 and 96 ppm. and pH varied from 8.1 to 9.8. A decreasing trend in alkalinity and increasing trend in pH was observed in all ponds. The mean hydrogen ion concentration for the entire period varied very little from pond to pond.

Mean pH values were as follows: pond A--9.03; pond B--9.25; pond C--9.3; pond D--9.1.

The dissolved oxygen concentrations in the ponds ranged from a maximum of 14.97 mg./1. in pond B to a minimum of 8.04 mg./1. in pond D. The dissolved oxygen trend was quite similar in each pond. There was an initial period of low oxygen concentration followed by an increase to a maximum on August 1. Following this peak, oxygen values remained high but fluctuated considerably for the duration of the study.

Influence of draining the ponds upon chemical conditions

Draining the ponds prior to the study apparently had a pronounced influence upon the concentration of nutrients in the water. It is well known that allowing ponds to dry and lie fallow releases nutrients from bottom soils (Mortimer and Hukling, 1954).

The total phosphorus concentration in all experimental ponds reached a peak on precisely the same date (Fig. 1) indicating that some factor was operating simultaneously in all ponds to bring phosphorus into solution. This peak might have been attributed to the addition of chelate and fertilizer in those ponds receiving this treatment were it not for the fact that the control pond not only exhibited this peak but nearly equaled the phosphorus concentration recorded in the ponds receiving artificial enrichment (see Fig. 1). This peak in phosphorus concentration is almost certainly an effect produced by drying and disturbing the bottom mud, and by release of phosphorus following

Figure 1. --Total phosphorus concentration in ponds in 1960.

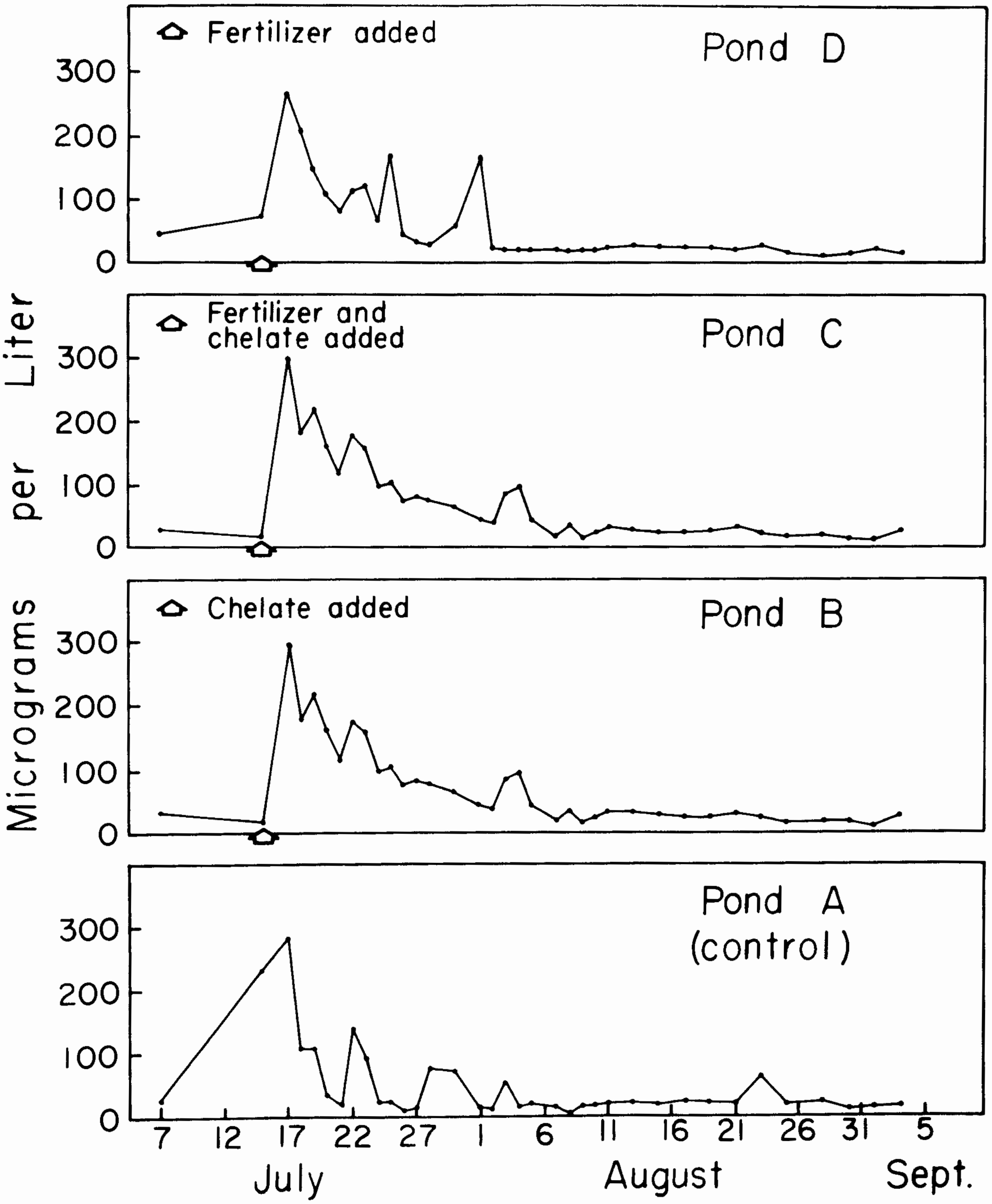
Fertilizer added
Pond D
Fertilizer and chelate added
Pond C
Chelate added
Pond B
Pond A (control)
Micrograms per Liter
300
200
100
0
7
12
17
22
27
1
6
11
16
21
26
31
5
July
August
Sept.

Figure 1

decomposition of the bottom vegetation. An excess of phosphorus over the actual needs of the plankton algae and bottom vegetation may have been present for a short time at the onset of the study period (Fig. 1), but, as the bottom vegetation began to flourish the concentration of phosphorus in the water steadily diminished, until a plateau level was reached in all ponds.

A situation similar to that observed for phosphorus developed in the case of iron. With fallowing and with death and decay of the aquatic plants, there seems to have been return of iron to the water. Thus we believe that if there were any effects produced by the chelating agent and fertilizer upon iron and phosphorus concentrations, these effects were masked by large releases of iron and phosphorus that occurred upon re-flooding.

Periphyton production

The term periphyton, as used in this paper is defined by Odum (1959) as; "organisms, both plant and animal, attached or clinging to stems and leaves of rooted plants or other surfaces projecting above the bottom." The composition of the periphyton biocoenosis living on the artificial substrates in the ponds was as follows: most abundant forms were representatives of the green algae, such as *Oedogonium*, *Bulbochaete*, *Scenedesmus*, *Tetraedron* and *Oocystis*; desmids (*Cosmarium*, *Micrasterias* and *Staurastrum*) were somewhat less abundant; diatoms, such as *Nitzschia*, *Fragilaria*, *Cymbella* and *Diatoma* were encountered only occasionally.

Net production was measured in all ponds for the period from June 24 to September 1, 1960 (Table 1). Each pond followed a slightly different week-to-week trend in accrual of organic weight, but a similar general trend was

Table 1. --Net primary production as determined by periphyton accrual on artificial substrata (ash-free dry weight)

Collection date (1960)	Exposure period (days)	Net production (grams per sq. meter per day)							
		Mean				Standard deviation			
		Pond				Pond			
		A	B	C	D	A	B	C	D
7-5	12	0.212	0.190	0.278	0.301	0.032	0.016	0.043	0.028
7-14	9	0.298	0.259	0.290	0.331	0.000	0.026	0.068	0.003
7-21	7	0.390	0.332	0.690	0.522	0.039	0.010	0.054	0.017
7-28	7	0.390	0.337	0.528	0.417	0.094	0.025	0.017	0.019
8-4	7	0.450	0.297	0.586	0.394	0.031	0.026	0.091	0.012
8-11	7	0.428	0.325	0.404	0.437	0.036	0.051	0.018	0.035
8-18	7	0.394	0.372	0.395	0.411	0.031	0.030	0.063	0.032
8-25	7	0.266	0.332	0.394	0.351	0.038	0.034	0.008	0.032
9-1	7	0.296	0.242	0.265	0.280	0.011	0.034	0.002	0.029
Mean		0.347	0.298	0.426	0.383				

observed in all ponds. Low production in the latter part of June and the first part of July was followed by maximum production during midsummer and a decline in production in late August and early September. Mean net production rates for the summer were as follows: in pond A it was estimated to be 0.347 grams ash-free dry weight per square meter per day; in pond B it was 0.298; in pond C it was 0.426; and in pond D it was 0.383 grams of ash-free dry weight per square meter per day. These values represent production during the summer, hence are probably much higher than a yearly average.

Production by aquatic macrophytes

The principal macrophytes in the ponds, in order of their importance are as follows: *Chara* sp.; *Potamogeton pectinatus*; *Potamogeton zosteriformis*; *Potamogeton natans*; *Carex* sp.; *Scirpus* sp.; *Typha latifolia*; *Sagittaria* sp.; *Elodea canadensis*; *Equisetum fluviatile*; *Eleocharis* sp.; and *Najas flexilis*.

The mean net productivity value obtained for each pond is given in Table 2. Values ranged from a high of 6.00 grams dry weight per square meter per day in pond D to a low of 1.45 grams dry weight per square meter per day in pond A.

Phytoplankton productivity

The predominant planktonic forms were rotifers, desmids and flagellates. Rotifers were represented by *Keratella* sp. and *Notholca* sp. Desmids were represented by *Cosmarium* sp., *Staurastrum* sp. and *Micrasterias* sp. Flagellates were represented by the dinoflagellate (*Ceratium hirundinella*, Stein), and three genera from the order Volvocales (*Eudorina* sp., *Pleodorina* sp. and *Volvox* sp.). Other forms frequently observed were copepods and

Table 2. --Net primary production of pond macrophytes during the 1960 growing season, as determined by the harvest method

Pond		Weight: Mean: Pounds per acre	Weight: Mean: Grams per sq. meter per day	Weight: Mean: Grams per sq. meter	Weight: Standard deviation: Grams per sq. meter
A	Wet	11,771		1,322	107
	Dry	1,047	1.45	118	42
B	Wet	38,533		4,326	330
	Dry	2,360	3.27	265	86
C	Wet	25,274		2,838	530
	Dry	2,042	2.83	229	181
D	Wet	22,272		2,501	331
	Dry	4,329	6.00	486	263

cladocera. The copepods were chiefly *Macrocyclops* sp., whereas the cladocera were represented by *Bosmina* sp. Diatoms were rare in the pond plankton samples.

The radioactive carbon method used in the present study yields a measure of photosynthesis that is somewhere between the net and gross value, possibly nearer to the former (Strickland, 1960). These data are presented in tabular form in Table 3. A maximum carbon assimilation value of 23.7 milligrams of carbon per cubic meter per hour was recorded in pond D at the exposure depth of 16 inches on July 24, 1960. The minimum carbon assimilation value was 2.75 milligrams of carbon per cubic meter per hour in pond A on July 10, 1960, at a depth of 32 inches.

Comparison of production estimates

Production rates as measured by the methods outlined above show variations from pond to pond (Table 4). There is, however, a close agreement in the order of various ponds when they are ranked using the C^{14} method and using the dry weight of macrophytes. Both of these estimates suggest that pond A is least productive, followed by pond C. Pond B has a somewhat greater mean production than either pond A or C, but is considerably less productive than pond D. The four ponds cannot be ranked in the same order using the periphyton method of measuring primary production. The periphyton method indicates that the lowest production rate occurred in pond B and the highest in pond C. Ponds A and D were intermediate. An estimate of total accrual of periphyton in the ponds cannot be calculated without information on the average area of substrata suitable for colonization. Thus rates of

Table 3.--Primary production measurement in ponds using the C^{14} method. One dark bottle and two light bottles were exposed for six hours at each depth.

[Assimilated carbon is expressed as milligrams of carbon per cubic meter per hour.]

Exposure date	Pond								Weather conditions during exposure	Water temperature during exposure (degrees F.)
	A		B		C		D			
	Depth (inches)		Depth (inches)		Depth (inches)		Depth (inches)			
	16*	32	16	32	16	32	16	32		
7-20-60	4.35	4.42	6.66	8.90	12.54	12.68	7.29	11.16	Very bright, clear	74
7-27-60	4.86	3.52	6.05	4.83	9.36	6.11	8.41	12.71	Clear, few clouds	78
8-3-60	5.83	4.32	12.44	10.27	10.46	8.69	14.83	15.60	Partly cloudy	79
8-10-60	3.68	2.75	7.68	7.57	8.66	7.53	14.35	15.15	AM--overcast PM--partly cloudy	73
8-17-60	7.87	6.82	10.17	9.15	8.36	9.59	15.76	22.60	AM--clear PM--overcast	74
8-24-60	4.89	4.36	7.72	7.76	9.30	6.90	23.75	22.70	AM--clear PM--overcast	76
8-31-60	7.44	7.96	11.59	9.15	8.26	6.83	11.37	10.60	Overcast to partly cloudy	78
9-7-60	7.11	7.14	11.33	13.76	8.90	8.68	18.38	11.99	Slightly overcast	82
Mean value	5.75	5.17	9.21	8.92	9.48	8.38	14.27	15.31		
Mean of 16- and 32-inch depths	5.46		9.07		8.93		14.79			

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* All exposure depths were measured from the surface of the pond to the sample.

Table 4. --Comparison of primary productivity estimates for various ecosystems

Location	Method	Production rate				Source
		Grams of organic matter per sq. meter per day		Macrophytes (dry weight)		
		Phytoplankton	Periphyton	Grams per sq. meter per day	Pounds per acre	
Pond A		0.30	0.35	1.45	1,047	
Pond B		0.48	0.30	3.27	2,360	
Pond C		0.44	0.44	2.83	2,042	
Pond D		0.64	0.38	6.00	4,328	
Blind Lake, Michigan		1.20				Schelske, 1960
Barents Sea	C^{14}	0.56				Corlett, 1957
North Sea (annual range)	C^{14}	0.20-3.00				Steel, 1957
South Atlantic	C^{14}	1.00-8.00				Steeman Nielsen, 1954
Red Cedar River, Michigan	Periphyton accrual		0.56			Grzenda, 1960
Silver Springs, Florida	Organic weight			7.40		H. T. Odum, 1957
Sargasso Sea	Organic weight			0.26		Riley, 1957
Seaweed beds, Nova Scotia	Harvest			1.00		Tamiya, 1957
Wheat (world average)	Harvest			2.30		Woytinsky and Woytinsky, 1953
Green Lake, Wisconsin	Harvest				1,590	Rickett, 1924
Lake Mendota, Wisconsin	Harvest				1,801	Rickett, 1922

accrual on artificial substrates are only indices of the intensity of this source of production. If the heavy growth of macrophytes in pond D provided the largest surface area for periphyton growth, then this pond might have had the highest total of periphyton production.

Table 4 gives some estimates of primary production in other ecosystems as well as a summary of estimates for the ponds. Values for production in terms of carbon have been converted to organic matter using a factor of 2.0 (Ryther, 1946). Comparing phytoplankton production of the ponds with other ecosystems suggests that production is comparatively low in the ponds. The ponds compare favorably with primary production reported for some parts of the ocean and with values reported for an unproductive lake in Michigan (Blind Lake). Since the ponds are much shallower than the other habitats a low production rate is to be expected when production is calculated on an areal basis. Periphyton accrual rates are similar to those observed in a warm water stream in southern Michigan (Table 4). Net production of larger plants in the most productive ponds was 2.4 times greater than that in Lake Mendota and 2.7 times greater than that in Green Lake (Table 4). Since these Wisconsin lakes are of high productivity it would seem that the level of production by aquatic macrophytes in the ponds is relatively high.

From the foregoing it would appear that production rates of phytoplankton in these ponds are low and rates of production by larger plants are rather high. It is hypothesized that the comparatively low production rates of phytoplankton as compared to macrophytes can be explained in terms of adaptive mechanisms available to larger plants and absent in phytoplankton. The rate of photosynthesis by phytoplankton cells is strongly influenced by light intensity. It increases with increasing intensity until a saturation value is reached. Above the saturation value, the rate remains constant with increasing intensity up to a critical intensity at which it decreases due to light inhibition of the photosynthetic process (Strickland, 1960). Inhibition is brought about by photooxidation of critical enzyme systems (Steeman Nielsen, 1952c). At high intensities, there is a bleaching of the chlorophyll in algal cells.

In shallow, transparent ponds the light intensity at all depths is a large fraction of that reaching the surface. According to Oosting (1958), in the presence of intense light larger plants exhibit elongated palisade cells. Cutin is thicker and the amount of supporting tissue is greater in intense light. Oosting (_ibid._) indicates that during intense illumination chloroplasts arrange themselves along the side walls of palisade cells, thus they receive a minimum of direct insulation. The possession of mechanisms adapting aquatic macrophytes to intense light may have enabled them to grow in luxuriant beds, while the phytoplankton, without such mechanisms, may have been light inhibited. Flooding ponds in early summer when there is little cloudiness may favor growth of aquatic macrophytes as compared to phytoplankton whereas the lower light intensities of a cloudy spring may favor growth of phytoplankton.

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