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(With Three Plates)

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EFFECTS OF INTENSITIES AND WAVE LENGTHS OF LIGHT ON UNICELLULAR GREEN ALGAE[1]

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INTRODUCTION

Unicellular green algae are admirably adapted to the study of the effectiveness of light intensity and light of different wave lengths on chlorophyll formation and on growth as defined by multiplication of cells. Their chief advantages as subjects of experimentation are: (1) their small size, the mechanism of photosynthesis being complete in the microscopic individual with its green chloroplast; (2) the uniformity of their surfaces, since each cell in those varieties that do not form zoospores may be considered comparable to every other one placed in a symmetrical environment; (3) their mode of growth in nutrient solution; and (4) the comparative ease of controlling the temperature and humidity conditions.

Control of the environment of algae as regards culture medium, temperature, and illumination was made the primary consideration in these experiments conducted in an effort to determine the reaction of algae to light. The importance of controlled conditions especially in matters of light intensity and wave length is easily seen when one reads through the literature. A few results of other investigators are reviewed.

I wish to express my deep appreciation to Dr. C. G. Abbot, Secretary of the Smithsonian Institution, and to Dr. Earl S. Johnston, Assistant Director of the Division of Radiation and Organisms, for their assistance in the completion of this piece of research. I am also very grateful to the other members of the Division of Radiation and Organisms, whose united efforts have made possible these experiments.

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RESULTS OF PREVIOUS INVESTIGATIONS

As early as 1861 Sachs (1864) originated the well-known method of growing plants in double-walled glass cylinders to determine the effects of colored lights. The cylinders contained respectively solutions of ammoniacal copper oxide for blue light, and potassium dichromate for orange light. No coloring solution was used with the third cylinder. He reported that plants needed from 4 to 6 days more in blue light than in orange light to unfold their leaflike cotyledons which remained smaller in the former so that the lamina in orange light was 2 to 3 times larger than in blue light, but largest of all in white light. Regarding leaf formation, the orange light acted as a lesser, the blue as a higher, degree of darkness. There was no formation of organic substance in the blue light, while a small amount was formed in orange light.

Pfeffer (1871) also working with double-walled cylinders of solutions found the following percentages of growth under the filters: 46.1 percent, yellow; 32.1 percent, red and orange; 15.0 percent, green; and 7.6 percent, blue, violet, and indigo. Later, in 1872, working with a prism he again found the maximum growth in the yellow.

Weber (1875) working with colored glasses as filters obtained similar results but in the following different percentages: 82.6 percent, yellow; 35.5 percent, red: 22.4 percent, blue; and 14.5 percent, violet.

Wiesner (1877) used a filter of potassium dichromate which transmitted the less refrangible half of the spectrum: red, orange, yellow, and a part of green; and also ammoniacal copper oxide which allows the passage of the remainder of the visible rays, the rest of the green and all of the blue and violet. He observed that the plants in weak light became greener sooner under yellow but in strong light sooner under blue. He believed rapid destruction accompanies chlorophyll formation in strong yellow or strong blue light which might not act directly upon the chlorophyll already formed but might have a harmful effect upon some process antecedent to chlorophyll formation.

Zachariewicz (1895), Flammarion (1897), and Strohmer and Stift (1905) agree that the maximum chlorophyll production is in the yellow rays.

Artari (1899) observed that blue-violet light accelerated the development of *Chlamydomonas ehrenbergii*.

Teodoresco (1899) using filters made up of chemical solutions studied the growth of corn in regions of the spectrum corresponding to the general chlorophyll absorption bands. Growth was found to be

best in the blue and violet, 5220 to 4260 A; less favorable in the red and a small part of the orange, —— to 6130 A; and poorest in the green, 5680 to 5240 A. Chlorophyll was present in all the regions of the spectrum studied separately.

Thirty years later Teodoresco (1929) reports about 170 experiments in which he investigated two main regions of the visible spectrum, using both colored solutions and glass filters. He measured the energy transmitted through both sets of filters by means of a thermopile and a galvanometer and equalized the intensities. In measuring the light intensity he used a screen of water and copper acetate to eliminate the effect of the infrared radiation. Using a variety of hepatics, vascular cryptogams, and phanerogams, Teodoresco found that in the red-orange, 7750 to 6440 A, the general configuration of the plant was abnormal, while in the blue, 5090 to 3660 A, the general appearance of the plant was normal and similar to plants grown in the shade or in white light. Fern germination was retarded in the blue light.

Nadson (1910) grew *Stichococcus bacillaris* Naegeli under bell jars of colored solutions and found that red-yellow light caused abnormally shaped cells and disorganized chromatophores of a pale yellow-green color. Cultures, 3 to 6 months old, grown in blue light finally attained a stage of development similar to the cultures in white light which were more normal in color and morphology.

Otto Thelen (1910), growing oats, beans, and other plants under light filters, obtained maximum production in the bright yellow and yellow-red light; the bright red light gave more than a third less dry weight, the blue still less, and the red and dark red, the least. The plants grown in white light produced almost as much dry weight as those grown under the yellow-red filter.

Dangeard (1912) immersed a piece of white blotting paper into a culture flask of *Chlorella vulgaris* growing in Knop solution, stretched it on the wall of a culture dish, and radiated it in a quartz spectrograph. The maximum action of the rays as indicated by the differences of vegetation was in the chlorophyll absorption bands. The algae grew best in the region 6700 to 6600 A, less in regions 6800 to 6700 A and 6600 to 6300 A, with a feebler growth in 6300 to 6000 A, and a very feeble growth in the range 6000 to 5700 A. No trace of the alga was visible from 5200 to 4000 A.

Klebs (1916-1917) showed that very striking formative changes can be induced in prothallia placed in different regions of the visible spectrum. He indicated that intensity and duration of light as well

as other environmental factors may bring about similar effects. This demonstrates the importance of measuring or recording all these factors in any study of the effect of light on plants.

Schanz (1919) grew higher plants in eight beds covered with various kinds of glass. In the first five beds the range of wave lengths of light transmitted was gradually decreased from the violet end of the spectrum toward the red, thus making possible the study of the effect of light from which greater and greater regions of the spectrum were eliminated in the blue-violet end. Combinations of colored glasses which gave predominating colors of yellow, green, and blue-violet were used in the last three beds. He found that chlorophyll development in beans, soybeans, and potatoes was more rapid the more the short rays were cut off, being most rapid under red light. In lettuce, chlorophyll developed fully under blue-violet rays but not in normal quantity in yellow or green light. Schanz did not measure the light intensity, nor does he give accurate information concerning temperature and other factors that possibly varied under the different types of glass.

Popp (1926) grew a number of higher plants in greenhouses under glasses transmitting only definite regions of the spectrum. The plants receiving no wave lengths shorter than 5290 A or 4720 A had a good development of chlorophyll and were somewhat similar to those grown under reduced light intensity. There was very little difference between plants that received all the rays of the spectrum of daylight and those from which only ultraviolet rays were eliminated. Popp claims that light intensity was not an important factor in his experiment for the following reason: The plants grew normally and vigorously in the full spectrum of daylight at an intensity that was at all times lower than that of the house in which all wave lengths shorter than 4720 A were removed and only slightly greater than that of the house in which wave lengths shorter than 5290 A were eliminated.

Sayre (1928) investigated the development of chlorophyll in seedlings under Corning glass ray filters and found that wave lengths of radiant energy longer than 6800 A are not effective in the formation of chlorophyll in corn, wheat, oats, barley, beans, sunflowers, and radishes, but that all other regions of the remaining visible and ultraviolet spectrum to 3000 A are effective provided the energy value is sufficient. For approximately equal energy values in these regions the red rays are more effective than the green and the green than the blue. The effectiveness of radiant energy seems to increase with the wave length to about 6800 A, where it ends abruptly.

Meier (1929), while working in Professor Chodat's laboratory, conducted a preliminary light experiment in conjunction with an experiment relating to the formation of carotin in green algae. Three series of cultures of *Chlorella rubescens* planted on solid media, Detmer $\frac{1}{3}$ plus glucose 2 percent with agar 1.5 percent, were placed at a north window; one in the modified diffused light, the second in violet light in a Senebier jar containing copper sulphate, and the third in yellow-orange light, in a Senebier jar containing potassium dichromate. Chlorophyll production followed by formation of carotin, and growth of the cells progressed most rapidly in natural light and least rapidly in the violet light. These results agree with those reported by Sachs on higher plants.

Arthur (1930) observed that plants grown under a red glass filter transmitting no blue light resembled those grown in a dark basement except that chlorophyll developed. The plants under a blue glass filter transmitting no red were dwarfed but otherwise normal.

I. EFFECTS OF DIFFERENT INTENSITIES

DESCRIPTION OF APPARATUS

To determine simultaneously the effect of different light intensities on algae under exactly similar conditions of medium and temperature, a large metal table similar to the one pictured in plate 1, figure 1, was constructed with four glass-bottomed water baths, each holding eighteen 300-cc Erlenmeyer flasks. The four water baths are connected to a centrally located thermostated mixing chamber which kept the temperature for these experiments at 21° C. In order to insure uniform dispersion of the algae, a common driving mechanism continuously agitates the Erlenmeyer flasks. The cultures are illuminated from below by artificial light from Mazda daylight lamps.

PRELIMINARY EXPERIMENT

A preliminary experiment was conducted to determine the best growing conditions and the nutrient solution best suited to the algae in this apparatus. The following solutions were prepared:

1. Detmer (Modified Koch Solution)

Calcium nitrate	1.	gram
Potassium chloride	0.25	"
Magnesium sulphate	0.25	"
Potassium acid phosphate	0.25	"
Iron	0.002	"
Distilled water	1 liter	

This solution made up in the above proportions was diluted to one-third.

2. Emerson's (1929) Solution

Magnesium sulphate .....0.01 molar
Potassium nitrate .....0.0125 "
Potassium acid phosphate.....0.0090 "
Calcium carbonate .....0.0001 "
Iron [a]

3. Johnston's (1929, 1932) Solution

Calcium nitrate .....0.005 volume molecular concentration
Magnesium sulphate .....0.002 " "
Potassium acid phosphate.....0.002 " " "
Distilled water made up to 1 liter
Iron [a]

4.

Detmer $\frac{1}{3}$ solution in which potassium chloride is replaced by .33 grams of potassium acid carbonate which supplies the same amount of potassium.

5.

Detmer $\frac{1}{3}$ solution in which potassium chloride is replaced by .6 grams of potassium acid carbonate.

6.

Detmer $\frac{1}{3}$ solution in which potassium chloride is replaced by 1.2 grams of potassium acid carbonate.

7.

Detmer $\frac{1}{3}$ solution in which potassium chloride is replaced by 2.4 grams of potassium acid carbonate.

8.

Similar to 1 but with cotton plugs.

9.

Similar to 2 but with cotton plugs.

[a] An equal quantity of iron was added to all the solutions.

Rubber stoppers were used for all the Erlenmeyer flasks except in 8 and 9, duplicate cultures of Detmer $\frac{1}{3}$ and Emerson respectively, which were plugged with cotton. The excess sulphur was removed from the rubber stoppers with petroleum ether before they were sterilized. One hundred cc of nutrient solutions was placed in each 300-cc Erlenmeyer flask and sterilized in an autoclave at 20 pounds pressure for 20 minutes.

Five cultures of each of the above solutions were inoculated with *Stichococcus bacillaris* Naegeli. A similar number of cultures was inoculated with *Chlorella vulgaris* var. Four sets of each alga were placed in the water baths, the fifth in a north window of the Smithsonian flag tower.

For this experiment, a 300-watt Mazda daylight lamp was placed under each of the four water baths. Under baths 1, 2, and 3 the bulb was placed so that the filament was 20 centimeters from the glass bottom of the bath. For bath 4 the distance was 40 centimeters. In bath 1 the cultures were stationary; the cultures in the other three baths were continuously agitated so that the cells were more evenly dispersed in the culture media. Cultures in baths 1, 3, and 4 were lighted continuously throughout the experiment, but those in bath 2 were illuminated for 6 hours daily from 1 a.m. to 7 a.m.

This experiment was of one month's duration from June 19, 1931, to July 17, 1931.

RESULTS

A. As regards growing conditions.—

1. The best development took place in those cultures grown under natural conditions of light and darkness in a north window of the tower.

2. Of the cultures grown under artificial conditions in the baths, the best ones were those grown in intermittent light at about a distance of 20 centimeters from the light.

3. The next best Detmer cultures were those grown in bath 4 at a distance of about 40 centimeters from the light.

4. The cultures in baths 1 and 3 gave the poorest results. There was continuous illumination at a distance of about 20 centimeters in both of these baths and in one set the cultures were stationary and in the other, continually shaking.

B. As regards solutions.—

1. The cultures of Detmer $\frac{1}{3}$ both with rubber stoppers and cotton plugs showed the best growth and most normal cells under all the different conditions.

2. All the other cultures showed poor growth under continuous light at 20 centimeters distance from the light in baths 1 and 3.

3. The cultures in which the potassium chloride of the Detmer solution was replaced by potassium acid carbonate did not give as good results as the Detmer $\frac{1}{3}$ solution.

4. The algae in the Johnston solution were a brighter green than the algae in the Detmer solution in the tower cultures.

5. The most normal algal cells occurred in the Emerson, Johnston, and Detmer solutions in the tower and in intermittent light, bath 2.

6. The cells of the stationary cultures were irregularly shaped and showed abnormally cut plastids.

7. The cells in the cultures 20 centimeters from the light, continuously illuminated, were very tiny.

CONCLUSIONS

1. Intermittent light gives more favorable results than continuous light.

2. In continuous illumination better results were obtained by the weaker light (at a distance of 40 centimeters).

3. Agitation is favorable to a more equal distribution of cells and hence a more uniform lighting condition. It also favors multiplication, as the cells do not collect in large masses.

4. Detmer $\frac{1}{3}$ is a favorable solution for the growth of the algae under the controlled conditions described above.

5. Rubber stoppers serve as well as cotton plugs in 300-cc flasks containing 100 cc of solution for an experimental period of a month.

SECOND EXPERIMENT

A second experiment was carried out with cultures of the following 15 algae: *Coccomyxa simplex, Chlorella viscosa, Scenedesmus flavescens, Chlorella vulgaris, Stichococcus bacillaris, Palmellococcus protothecoides, Oocystis naegelii, Cystococcus irregularis, Chlamydomonas intermedia, Palmelococcus variegatus, Chlorococcum viscosum, Scenedesmus chlorelloides* var., *Chlorella vulgaris* var., *Cystococcus cohaerens,* and *Heterococcus viridis.* Three sets of the cultures were illuminated each by a 300-watt Mazda daylight lamp at a distance of 40 centimeters from the glass bottom of the bath to the top of the filament of the lamp. The fourth was kept in darkness.

Of the three illuminated culture sets, one received intermittent light for 6 hours. All the cultures were constantly agitated with the exception of one of the two receiving continuous illumination. The experiment was in progress from July 28 to August 18, 1931. Detmer $\frac{1}{3}$ solution was used for each alga.

The cultures that were agitated continuously and lighted intermittently and the cultures that were stationary and lighted continuously produced the most satisfactory results at the end of the experimental period. In the stationary cultures, the algae had formed a film on the bottom of the glass flasks that shielded those in the solution from the intense light. The first seven algae listed above were greenest and in the best condition. The next six listed were less green probably because the light was too intense, while the last two listed, that is, *Cystococcus cohaerens* and *Heterococcus viridis,* were killed by the intense light in all three of the baths.

The cultures which were continually agitated and kept as closely as possible in continuous darkness gave the following results: all

the algal suspensions were practically colorless in appearance, but by microscopic examination some green cells mixed with numerous colorless cells were found for the following eight varieties: *Stichococcus bacillaris, Chlorella vulgaris, Scenedesmus chlorelloides* var., *Oocystis naegelii, Chlorella viscosa, Scenedesmus flavescens, Cystococcus irregularis* and *Palmellococcus variegatus.* All colorless cells were found in the following four varieties: *Palmellococcus protothecoides, Coccomyxa simplex, Chlorella vulgaris* var., and *Chlamydomonas intermedia.*

THIRD EXPERIMENT

In the third experiment, which was in progress from October 10 to November 9, 1931, all the cultures in the four baths were constantly agitated and lighted continuously. Mazda daylight lamps were used and were so placed that the ratios of intensities in the four baths were 1 : 3 : 9 : 27.

Bath	Wattage	Distance [a]	Intensity [b] microwatts/mm [2]	Ratio
1	60 (frosted)	5.95	3.76	1.00
2	200	36.7	11.5	3.06
3	300	35.9	34.1	9.06
4	300	18.8	102.0	27.0

[a] The distance was measured from the glass bottom of the bath to the top of the filament of the lamp.
[b] As measured with a thermocouple.

In addition to the algae listed in the second experiment, cultures of *Haematococcus pluvialis* and *Palmellococcus miniatus* were used. Microscopic counts were made of each culture at the beginning and at the end of the experiment.

The increase in number of cells was roughly proportional to the increase in light intensity in the cultures of *Oocystis naegelii, Palmellococcus protothecoides, Chlorella vulgaris, Palmellococcus miniatus, Chlamydomonas intermedia, Scenedesmus chlorelloides* var., *Heterococcus viridis, Chlorella viscosa, Cystococcus irregularis, Cystococcus cohaerens, Coccomyxa simplex,* and *Palmellococcus variegatus.* Four algae behaved differently. The most intense light caused the poorest development of *Stichococcus bacillaris* and *Scenedesmus flavescens,* although for the three other intensities the growth was proportional. The growth was inversely proportional to the light intensity in *Chlorella vulgaris* var. *Chlorococcum viscosum* grew very little in all four light intensities. Cells with green chloroplasts were present in all the cultures of the algae listed above. *Hematococcus pluvialis* had a few gray-green cells in the lowest light intensity, more green cells

in the next two light intensities, and numerous green cells with red eye spots and a number of completely orange-red cells in the highest light intensity.

II. EFFECTS OF DIFFERENT WAVE LENGTHS

THE PLANT USED

Stichococcus bacillaris Naegeli, the green alga used in this experiment, consists of a single cylindrical cell with rounded ends usually partially filled with the chloroplast. The dimensions of the cell vary from 2 to 2.5 μ in diameter and from 4 to 8 μ in length. Multiplication takes place by transverse division of the protoplast and the formation of cross walls. The nucleus usually lies near the center of the cell. (See pl. 2.) Filaments of cells were rarely observed in my cultures. The alga develops rapidly, soon forming a green deposit in Detmer $\frac{1}{3}$ containing 0.005 percent to 0.02 percent ferric chloride.

The cells multiply very slowly on a solid medium such as Detmer $\frac{1}{3}$ agar, and after two months' time small green buttons about 4 to 7 millimeters in diameter are present on the agar. If dextrose from 1.5 to 2 percent is added to the medium, the flat regular dark green disks may grow to over 1 centimeter in diameter.

This alga does not liquefy gelatine but forms a slight dark green growth on the surface of the culture medium.

My cultures have remained green in the dark for two months on Detmer $\frac{1}{3}$ agar plus 2 percent dextrose. The colonial formations, although greener, are smaller when grown in darkness than corresponding cultures in the light, owing to the less rapid development and exhaustion of the nutrient medium. Artari (1899), Radais (1900), Matruchot and Molliard (1902), and Chodat (1913), have also grown green cultures of *Stichococcus bacillaris* in darkness. Cultures illuminated continuously by electric light for two months were a brownish-gray color and the individual cells were abnormally shaped. Corresponding cultures in sky illumination showed normal cells but were beginning to discolor at the center of each colonial disk.

APPARATUS

A metal table somewhat similar to the one used for experimenting on the effects of light intensity was constructed for experimental work on the effect of light of different wave lengths on one variety of alga. (See pl. 1, fig. 1.)

This table was constructed with four glass-bottomed water baths each holding six 300-cc Erlenmeyer flasks. Each flask is enclosed in a container with a light filter on the bottom. (See pl. 3, fig. 2.) The holders containing the flasks are maintained in continuous agitation. Each filter is one of a duplicate series of 12 short wave length cut-off filters, that is, a set which transmits progressively shorter and shorter

TABLE 1.—*Short Wave Length Cut-off Filters* [a]

Name of filter	Cut-off A
Heat resisting pyrometer red, 62 percent	6000
Heat resisting red, 130 percent	5900
Heat resisting red, 245 percent	5800
Heat resisting lighthouse red, 100 percent	5600
Heat resisting yellow, red shade	5200
Heat resisting yellow, medium shade	5000
Heat resisting yellow, yellow shade	4800
Heat resisting Noviol	4600
Noviol "C"	4500
Noviol "O"	4000
Nultra	3700

[a] These filters are made by the Corning Glass Company.

wave lengths from one transmitting only deep red to the other extreme where the whole region is included, as shown in table 1. One special filter is included in each set. Each flask containing its inoculated culture of *Stichococcus bacillaris* was placed in the container, which cut out all light except that entering through the glass filter. For the sake of convenience, one set of cultures is indicated north side (N) and the duplicate set, south side (S).

EARLY EXPERIMENTS

Five experiments were conducted in this apparatus. The results of the first two experiments are questionable, since the light intensity measurements taken through the various filters at the close of the experiment were found to vary as much as 50 percent from the original measurements. The experiment was attempted a third time, care being taken to clean the flasks and filters daily and also to observe any change in light intensity with a photoelectric cell and to correct the intensity changes accordingly. After the experiment had run for 10 days, the belt of the motor governing the circulation of water broke during the night. By morning, the temperature of the cultures had risen to 120° F. and as the majority of the algal cells were found to be deformed, colorless, or exuding their chlorophyll, the results of this experiment were also discarded.

FOURTH EXPERIMENT

The apparatus was completely overhauled for the fourth experiment. This time a more trustworthy thermostat was used with a safety device for cutting off the heater and lights in case of accident. An electric clock was connected with the lighting system in such a manner as to indicate any length of time the apparatus was not functioning properly when the observer was absent.

Johnston's (1932) work with tomato plants grown under Mazda lamps indicates that a large proportion of infrared radiation present in this type of illumination is injurious to the plants. Heat-absorbing filters give more normal growth and physiological response, and where the excessive infrared radiation from the lamps is absorbed by a solution of copper sulphate, the plants are more normal. For this reason a solution of copper sulphate (1.007 specific gravity at 80° F.) was used in place of distilled water in the circulating system that controls the temperature of the four baths.

In the third light-intensity experiment on page 9 it was found that *Stichococcus bacillaris* increased in proportion to the increase in light intensity when the intensities measured through water were 3.76, 11.5, and 34.1 microwatts/mm^2. In this experiment, as well as in the fifth one, the intensity measured through the copper sulphate solution was 25 microwatts/mm^2. Since the intensity as measured through the copper sulphate solution is less than the next to the highest light intensity used in the third light-intensity experiment, we know that the light intensity in the filter experiments is favorable to the growth of these algal cells.

The copper sulphate solution entered each separate bath through a flaring glass tube, over the end of which was placed a bag of huck toweling. These bags strained out most of the bubbles caused by the central pump, as well as any dirt or grease present, thus keeping the copper sulphate solution clear in each bath.

Mazda lamps were used under each bath and so arranged at distances from the glass bottom of the bath that the light intensity was the same under each of the duplicate sets of 12 filters as measured by the thermocouple. Frequent readings of the light intensity were made during the experiment to insure the similarity of the intensity under the filters, and when necessary the distances of the lamps from the bottom of the bath were changed or the lamps replaced by new ones. The voltage was read at the same time the intensities were measured, since the voltage fluctuated slightly from day to day thus causing a difference in intensity. The Erlenmeyer

flasks, the filters, and the glass bottoms of the water baths were cleaned whenever necessary. While the filters were being cleaned, the culture flasks were kept in a covered dark box.

The temperature of the baths was regulated by a thermostat set at 21° C. throughout the experiment. The experiment was in progress from February 7 to March 24, 1933.

A uniform medium and uniform inoculation were insured for all the cultures by the following method: A 3-liter pyrex glass flask was fitted with a rubber stopper through which was inserted a large glass tube. One end of the tube was plunged in the culture medium, the other fitted in rubber tubing with a stopcock ending in a glass pipette. A second smaller glass tube was inserted through the rubber stopper, then connected to a compressed air tube by rubber tubes and a glass tube with cotton filters to filter out dust. (See pl. 3, fig. 1.) The culture medium Detmer $\frac{1}{3}$, for the 24 individual flasks was made up in this large previously sterilized flask, which was again sterilized in the autoclave at 20 pounds pressure for 20 minutes.

About 100 cc of a dark green suspension of cells of *Stichococcus bacillaris* that had been growing in a north window for one month was used to inoculate the 3-liter flask of Detmer $\frac{1}{3}$ solution. Twenty-four hours later the solution was well shaken and siphoned into each sterilized 300-cc flask to the previously marked 100-cc level.

Three extra cultures were placed in the north, south, and west windows of the tower. Samples of the inoculated medium were measured by the nephelometer, the pH was determined colorimetrically, and microscopic counts were made at the time when the flasks were adjusted in the baths and the experiment started. Microscopic counts, nephelometer measurements, and pH determinations were also made at the close of the experimental period. The results of this experiment are indicated in tables 2 to 9 and will be discussed in connection with those obtained in the fifth experiment.

FIFTH EXPERIMENT

A fifth experiment, a repetition of the fourth experiment with the exception of the duration, was carried on from May 29 to June 13, 1933. The results of this experiment are assembled with those of the fourth experiment in tables 2 to 9.

THE PH OF THE CULTURES

As Kostychev (1931) points out, the change of pH is a factor not to be ignored when stimulation or retardation of enzyme action, elec-

trical discharge of cell colloids, and the permeability of the plasma membrane and other physiological processes are at work in a culture. There is a certain range of pH in which each plant can exist. In the fourth and fifth experiments the pH of the cultures was measured at the beginning and at the end of the experiment with the Hellige comparator, which uses colored glass disks in place of the standard

TABLE 2.—*pH Determinations at End of Experiments*

Filter: short wave length cut-off	Fourth experiment (Original solution, pH 5.4)	Fifth experiment (Original solution pH 5.6)	
	North	North	South
A	pH	pH	pH
6000	5.2	5.8	5.2
5900	5.2	5.2	5.6
5800	4.8	5.4	5.4
5600	4.8	5.6	5.2
5200	4.8	5.2	5.6
5000	5.2	5.8	5.6
4800	4.8	5.8	5.6
4600	4.8		5.6
4500	4.8	5.8	5.8
4000	5.4	5.4	5.6
3700	4.8	5.4	5.8

solutions with which the sample of culture solution plus the indicator is compared. Inadvertently, the cultures grown on the south side of the water baths for the fourth experiment were discarded before the pH could be determined. In these experiments, as shown by table 2, the change in acidity of the cultures at the end of the experimental period as compared with the original acidity is negligible, the maxima being 0.6 pH in the fourth experiment and 0.4 pH in the fifth experiment.

THE NEPHELOMETER

A special type of nephelometer was constructed to compare the relative concentrations of the solutions. As shown in plate 1, figure 2, this piece of apparatus consists of two stationary glass cells in each of which is inserted a similar movable cell filled with distilled water enclosing a stationary glass plunger lined with black paper to prevent reflections. A beam of light is thrown on the glass cells from a condensing lens, and the cells are adjusted so that the light beam always passes through the same depth of liquid. Each movable glass cell is attached to a metric scale that gives the depth of the solution and is adjustable so that the depth of the unknown solution placed in the bottom stationary cell may change from zero to the length of the

scale. The intensity measurements are made with a photronic cell and galvanometer system.

A zero adjustment was made with the nutrient solution in the four cells so that there is equal intensity on both sides of the apparatus as shown by the deflection of the galvanometer. It was found that this intensity was practically independent of the depth of the nutrient solution. Then the nutrient solution in the bottom cell on one side is replaced by the freshly inoculated solution at a chosen depth, thus causing a deflection of the galvanometer less than that of the nutrient solution in the cells on the other side. The percentage change in the ratio of the two galvanometer deflections represents the absorption of the inoculated solution. After the experimental period the depth of each culture solution was adjusted to give the same ratio with the nutrient solution as did the original inoculated solution.

According to Beer's Law, the concentration of the solution is proportional to the logarithm of the intensity of the light transmitted through the various thicknesses; or if the ratio of the light falling on the cell to the light transmitted remains constant, the concentrations of the solutions are inversely proportional to the depth.

$$I = I_0 e^{-acx} \quad \text{(Beer's Law)}$$

where

I = Intensity of light transmitted by thickness x of nutrient solution plus algae

I_0 = Intensity transmitted by nutrient solution (no algae)

(I and I_0 are measured with the photronic cell)

x = thickness or length of column

c = concentration of algae

a = a constant depending on absorbing medium (we assume a is constant for the algae before and after growth in the experiment)

The procedure was usually to measure the intensity transmitted through the original inoculated solution and to call this I_s for a length x_s. Then after growth, x was adjusted to the same ratio.

$$\frac{I_s}{I_0} = \frac{I}{I_0} = k$$

then

$$\log_e \frac{I_s}{I_0} = \log_e \frac{I}{I_0} = \log_e k = K$$

and

$$\log_e \frac{I}{I_0} = acx = K$$

also

$$\log_e \frac{I_s}{I_0} = ac_s x_s = K$$

or

$$acx = ac_s x_s$$

so

$$\frac{c}{c_s} = \frac{x_s}{x}$$

i.e., the concentrations are inversely proportional to the length (x). Also

$$\frac{c}{c_s} = \text{growth,}$$

i.e., if

$$\frac{x_s}{x} = 3$$

then the increase or growth was 3 times.

RESULTS

TOWER CULTURES

The three cultures grown in natural conditions of light and dark in the tower gave the following results:

Window	Galvanometer deflection	Growth factor	Microscopic count	Microscopic growth ratio
North	55.1	.99	106.8	4.9
South	65.5	.83	92.4	4.2
West	52.5	1.04	116.0	5.3

The pH was 5.8 in all three cultures. The cultures in the north and south windows contained bright green cells, while those in the west window were pale green and many of the chloroplasts were shrunken and slightly abnormal. Possibly the afternoon sunlight in the heat of the day is too strong for the cells.

CHLOROPHYLL

Samples of each culture when examined microscopically at the end of the fourth and fifth experiments showed that chlorophyll was present in all the cultures. The chloroplastids in some cultures were in a more healthy condition than in others, as shown by table 3. In

TABLE 3.—*Description of Chloroplasts of Cells at End of Experimental Periods*

Filter: short wave length cut off	Fourth experiment		Fifth experiment	
	North side	South side	North side	South side
A				
6000	40% green and pale green 3% with yellow granules 57% colorless	48% green and pale green 48% greenish yellow 4% colorless	68% olive-green and greenish yellow 32% colorless, dark spots in some cells	green and faded blue-green
5900	23% green and pale green 62% with yellow granules 15% colorless	60% green and pale green 20% with yellow granules 20% colorless	84% green with yellow granules 12% very faded 4% colorless	bright green
5800	86% green 14% colorless	74% green and pale green 13% with yellow granules 13% colorless	pale sickly green	sickly green disintegrated
5600	50% green 50% colorless	38% pale green 21% with yellow granules 41% colorless	green with yellow granules	green with yellow granules
5200	15% green and pale green 58% with yellow granules 27% discolored and disintegrated	60% green and pale green 40% with yellow granules	very faded olive green	green
5000	31% green and pale green 59% with yellow granules 10% colorless	80% green and pale green 11% with yellow granules 9% colorless	68% bright green 20% orange 12% colorless	green lumps with yellow granules
4800	73% green 9% with yellow granules 18% colorless	68% green and pale green 20% with yellow granules 12% colorless	grass-green a few yellow-green	green lumps
4600	83% green 17% colorless	83% green and pale green 17% colorless	green and pale green	76% bright green 24% colorless
4500	100% green, most normal culture in this series	68% green 16% with yellow granules 16% colorless	grass-green and dark green	green
4000	67% green and pale green 22% with yellow granules 11% colorless	80% green 7% with yellow granules 13% colorless	very pale green	green, a few discolored
3700	93% green and 7% colorless	98% grass green 2% colorless	normal green	green with yellow granules

studying these tables, it should be borne in mind that the fourth experiment was in progress for a period of 45 days, whereas the fifth experiment was of 16 days' duration. The difference in time probably accounts for the greater number of colorless cells and cells in which carotin had begun to appear in the fourth experiment. It should be noted that cultures growing in light where the wave lengths were cut off at 3700, 4000, 4500, 4600, 4800, and 5000 A were in especially good condition.

The cultures that showed the most disintegration of the chloroplasts were those where the light was cut off at 5200 A in the fourth experiment, 5600, 5800, and 5900 A, with the exception of one culture in the fifth experiment, and 6000 A.

GROWTH AS INDICATED BY MULTIPLICATION OF CELLS

The results show that cell multiplication ranging from twofold to fourfold occurred in all the complex beams of radiation.

The third intensity experiment indicated that within the limits of intensity here employed multiplication is proportional to the intensity of illumination.

If it be assumed that this law holds for each of the complex beams employed, means are found for separating the propagating influences of different wave lengths. For if in the energy curves of two complexes whose included areas are equal a part P is common, then if Q be the total area of either curve and M the growth ratio due to the complex of longer wave lengths, $\frac{Q-P}{Q}M$ would be the growth ratio due to the part of the long-wave complex remaining in the shorter-wave complex. If N be the observed growth ratio of the shorter-wave complex, $N-\frac{Q-P}{Q}M$ will be the growth ratio due to the shorter wave lengths not found in the longer-wave complex.

Working on this plan, growth ratios have been computed for many narrow ranges of wave lengths, and by inspection of the overlapped energy curves, approximate values of their effective wave lengths have been estimated. (See tables 4-9.)

In this way it is found that a wide red and infrared complex of wave lengths from 0.6 to 1.4 microns is moderately effective in promoting multiplication of algae. It is impossible to know from these experiments which of its wave lengths are the most effective. The

other ranges of wave lengths show different results. Some appear to inhibit multiplication, while others seem greatly to enhance it.

Inasmuch as the results depend on difference computations as between determinations themselves of considerable probable error, these estimates of the effectiveness of different narrow ranges of wave lengths to promote algal multiplication are very uncertain, but are given for what they may be worth.

Growth experiments made with definite narrow ranges of wave lengths by the aid of Christiansen filters should give more conclusive results.

GENERAL CONCLUSIONS

Multiplication of the unicellular green alga, *Stichococcus bacillaris* Naegeli, is proportional to the intensity of illumination ranging from 3.76 to 34.1 microwatts/mm^2. A higher intensity than 34.1 microwatts/mm^2 such as 102.0 microwatts/mm^2 checks the growth of this alga.

Complex beams of radiation from 11 short wave length cut-off filters were used to transmit progressively shorter and shorter wave lengths from one transmitting only deep red, 6000 A, to the other extreme, 3700 A, where most of the visible region is included. Chlorophyll was formed under all the filters, but in best condition when the wave lengths of the blue-violet region were included.

A multiplication of algae ranging from twofold to fourfold was obtained in the cultures. By computing growth ratios for many narrow ranges of wave lengths and by estimating approximate values under the energy curves of the effective wave lengths it is found that a wide red and infrared complex of waves from 0.6 to 1.4 microns is moderately effective for the multiplication of the algal cells.

Some ranges of wave lengths appear to inhibit cell multiplication and chlorophyll formation. Some appear to favor them. Only by means of experimentation with isolated narrow ranges of light can the effectiveness of all the wave lengths be determined. A similar experiment with Christiansen filters instead of the glass ones is now in progress and should give more conclusive results.

TABLE 4.—*Microscopic Count of Algal Cells in Cultures at End of Experimental Period*

Filter: short wave length cut off	North side				South side			
	Fourth experiment		Fifth experiment		Fourth experiment		Fifth experiment	
	Final count	Final count ÷ 9 [a] to find N_4 ratio	Final count	Final count ÷ 22 [b] to find N_5 ratio	Final count	Final count ÷ 9 [a] to find S_4 ratio	Final count	Final count ÷ 22 [b] to find S_5 ratio
6000	40	4.4	116	5.3	23	2.5	80	3.6
5900	91	10.1	88	4.0	15	1.7	75	3.4
5800	117	13.	38	1.7	15	1.7	24	1.1
5600	46	5.1	133	6.0	29	3.2	185	8.4
5200	96	10.7	105	4.8	120	13.3	142	6.5
5000	145	16.1	62	2.8	131	14.5	98	4.5
4800	132	14.7	20	0.9	25	2.8	48	2.2
4600	120	13.3	57	2.6	36	4.	64	2.9
4500	100	11.1	45	2.0	57	6.3	48	2.2
4000	72	8.	46	2.1	15	1.7	42	1.9
3700	90	10.	100	4.5	66	7.3	136	6.2

[a] The original culture in the fourth experiment contained 9 cells.

[b] The original culture in the fifth experiment contained 22 cells.

TABLE 5.—*Computation Table Made to Find the Mean Microscopic Counts*

Filter: short wave length cut off A	Ratios of $N_4 \div$ ratios of N_5	Ratios of $S_4 \div$ ratios of S_5	N_4 ratios $\div$ 4.4	N_5 ratios	S_4 ratios $\div$ 1.7	S_5 ratios	Sums of relative ratios omitting wild ones	Mean omitting wild ones
6000	(0.8) [a]	0.7	(1.0)	5.3	(1.5)	3.6	8.9	4.45
5900	2.5	(0.5)	2.3	4.0	(1.0)	3.4	9.7	3.23
5800	7.6	1.5	3.0	1.7	1.0	1.1	6.8	1.70
5600	(0.9)	(0.4)	1.2	(6.0)	1.9	(8.4)	3.1	1.55
5200	2.2	2.0	2.4	4.8	(7.8)	6.5	13.7	4.56
5000	5.8	3.2	3.7	2.8	(8.5)	4.5	11.0	3.66
4800	(16.3)	1.3	3.3	0.9	1.6	2.2	8.0	2.00
4600	5.1	1.4	3.0	2.6	2.4	2.9	10.9	2.72
4500	5.6	2.9	2.5	2.0	3.7	2.2	10.4	2.60
4000	3.8	0.9	1.8	2.1	1.0	1.9	6.8	1.70
3700	2.2	1.2	2.3	4.5	4.3	6.2	17.3	4.32
Sum	34.8	15.1						

$$\frac{34.8}{8} = 4.35 \qquad \frac{15.1}{9} = 1.67$$

N_4 = North side of fourth experiment. N_5 = North side of fifth experiment. S_4 = South side of fourth experiment. S_5 = South side of fifth experiment.

[a] Results enclosed in parentheses are questionable and were omitted.

TABLE 6.—*Nephelometer Data of Algal Cultures at End of Experimental Period*

Filter: short wave length cut off	North side				South side			
	Fourth experiment		Fifth experiment		Fourth experiment		Fifth experiment	
	Galvanometer deflection mm	Growth factor	Galvanometer deflection mm	Growth factor	Galvanometer deflection mm	Growth factor	Galvanometer deflection mm	Growth factor
A								
6000	38.3	7.5	74.3	.73	22.8	12.5	67.4	.81
5900	38.2	7.5	60.0	.91	17.5	16.3	86.3	.63
5800	26.0	11.0	80.3	.68	33.1	8.6	83.5	.65
5600	30.4	9.4	72.5	.75	15.0	19.0	72.5	.75
5200	26.8	10.6	61.3	.89	31.7	9.0	102.0	.54
5000	28.3	10.1	106.0	.52	30.2	9.5	103.0	.53
4800	33.1	8.6	81.3	.67	39.2	7.3	66.9	.82
4600	25.0	11.4	45.5	1.20	24.4	11.7	104.0	.53
4500	21.8	13.1	66.0	.83	43.1	6.6	105.0	.52
4000	40.5	7.0	51.1	1.07	33.4	8.5	105.0	.52
3700	32.3	8.8	42.2	1.29	53.3	5.4	72.3	.76

[a] Fourth experiment. Galvanometer deflections made at 80 mm depth. The deflection of the original solution was 26.7 mm, that directly after inoculation was 23.83 mm.

[b] Fifth experiment. Galvanometer deflections made at 90 mm depth. The deflection of the original solution was 30.40 mm, that of the inoculated solution, 12.75 mm.

TABLE 7.—*Computation Made to Find the Mean Nephelometric Growth Factors*

Filter: short wave length cut off	Growth factors of $N_4 \div$ growth factors of N_5	Growth factors of $S_4 \div$ growth factors of S_5	N_4 growth factors ÷ 11.8	N_5 growth factors	S_4 growth factors ÷ 15.6	S_5 growth factors	Sums of relative growth factors omitting wild ones	Mean omitting wild ones
A								
6000	10.27	15.43	.64	.73	.80	.81	2.98	.745
5900	8.24	(25.87) [a]	.64	.91	1.04	.63	3.22	.805
5800	16.17	13.23	.93	.68	.55	.65	2.81	.702
5600	12.53	25.33	.80	.75	1.21	.75	3.51	.877
5200	11.91	16.66	.90	.89	.58	.54	2.91	.727
5000	19.42	17.92	.86	.52	.61	.53	2.52	.630
4800	12.83	8.90	.73	.67	.47	.82	2.69	.672
4600	9.50	22.07	.97	(1.20)	.75	.53	2.25	.750
4500	15.78	12.69	1.11	.83	.42	.52	2.88	.720
4000	6.54	16.34	.59	1.07	.54	.52	2.72	.680
3700	6.82	7.10	.75	1.29	.35	.76	3.15	.787
Sum	130.01	155.67						

$$\frac{130.01}{11} = 11.81 \qquad \frac{155.67}{10} = 15.56$$

[a] Results enclosed in parentheses are questionable and were omitted.

TABLE 8.—*Computation Made to Find the General Mean Algal Multiplication*

Filter: short wave length cut off	Mean microscopic counts ÷ mean nephelometric growth factors	Mean nephelometric growth factors × 4.0 [a]	Mean microscopic counts	Sums of relative means	General mean algal multiplication
A					
6000	5.97	2.98	4.45	7.43	3.71
5900	4.01	3.22	3.23	6.45	3.23
5800	2.42	2.80	1.70	4.50	2.25
5600	1.77	3.51	1.55	5.06	2.53
5200	6.28	2.91	4.56	7.47	3.74
5000	5.81	2.52	3.66	6.18	3.09
4800	2.98	2.69	2.00	4.69	2.34
4600	3.63	3.00	2.72	5.72	2.86
4500	3.61	2.88	2.60	5.48	2.74
4000	2.50	2.72	1.70	4.42	2.21
3700	5.49	3.15	4.32	7.47	3.74
Sum	44.47				

$$\frac{44.47}{11} = 4.04$$

[a] To reduce the mean nephelometric growth factors to the status of mean microscopic counts.

TABLE 9.—*Computation Made Assuming Algal Multiplication Proportional to Intensity*

Filter: short wave length cut off	General mean algal multiplication	Mean area ratio	Computed multiplication of longer waves	Effective multiplication of shorter waves	Divisor equals unity minus mean area ratio	Same for equal energy	Effective mean wave length μ	Wave length with ultraviolet weighting of curves
A								
6000	3.71				1.000	+ 3.7	1.00?	1.00?
5900	3.23	.940	3.48	— 0.25	0.060	— 4.1	.643	.643
5800	2.25	.917	2.96	— 0.71	0.083	— 8.6	.618	.618
5600	2.53	.972	2.19	+ 0.34	0.028	+ 12.1	.607	.605
5200	3.74	.983	2.49	+ 1.25	0.017	+ 73.5	.598	.590
5000	3.09	.917	3.43	— 0.34	0.083	— 4.1	.574	.562
4800	2.34	.943	2.91	— 0.57	0.057	— 10.0	.554	.540
4600	2.86	.924	2.16	+ 0.70	0.076	+ 9.2	.526	.500
4500	2.74	.972	2.78	— 0.04	0.028	— 1.4	.523	.490
4000	2.21	a	a	a	a	a	a	a
3700	3.74	.975	2.13	+ 1.61	0.025	+ 64.4	.507	.460

[a] Overlapping of absorption curves of filters hindered the completion of this computation.

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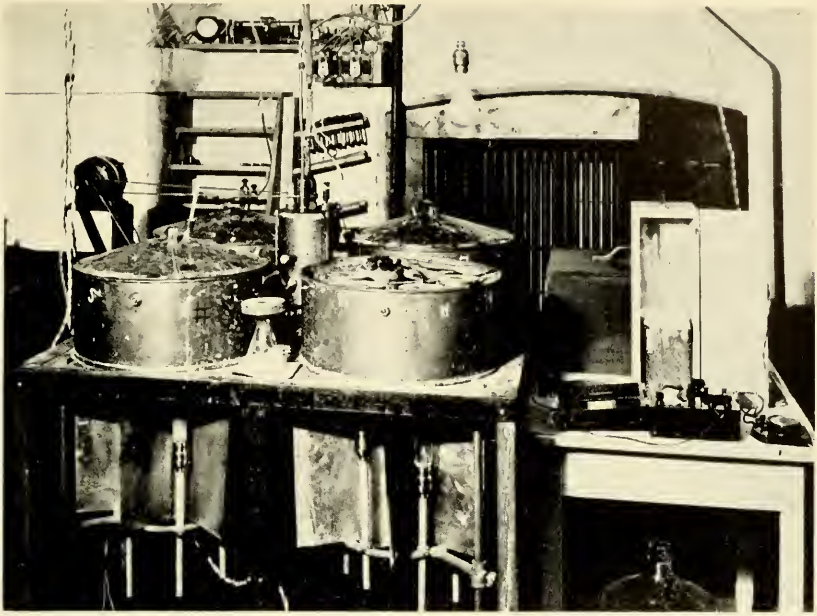
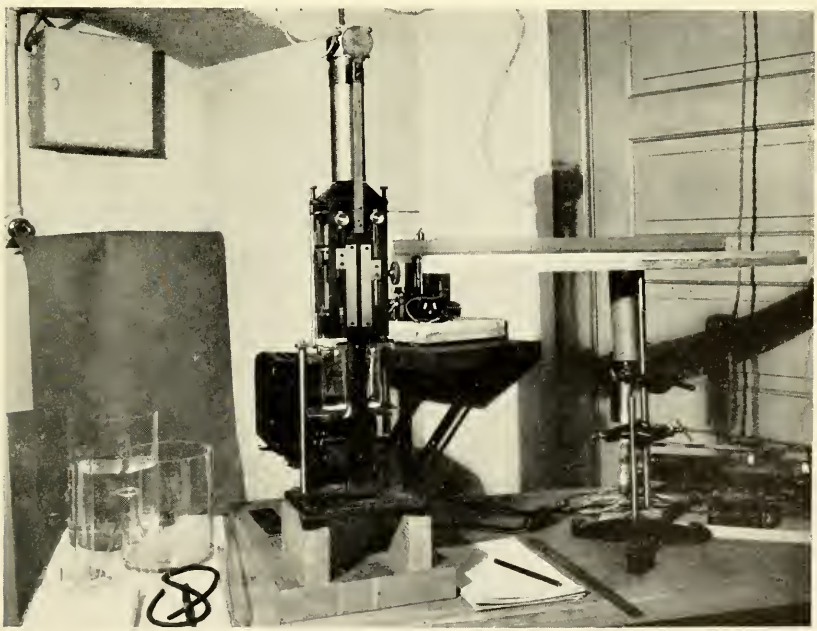
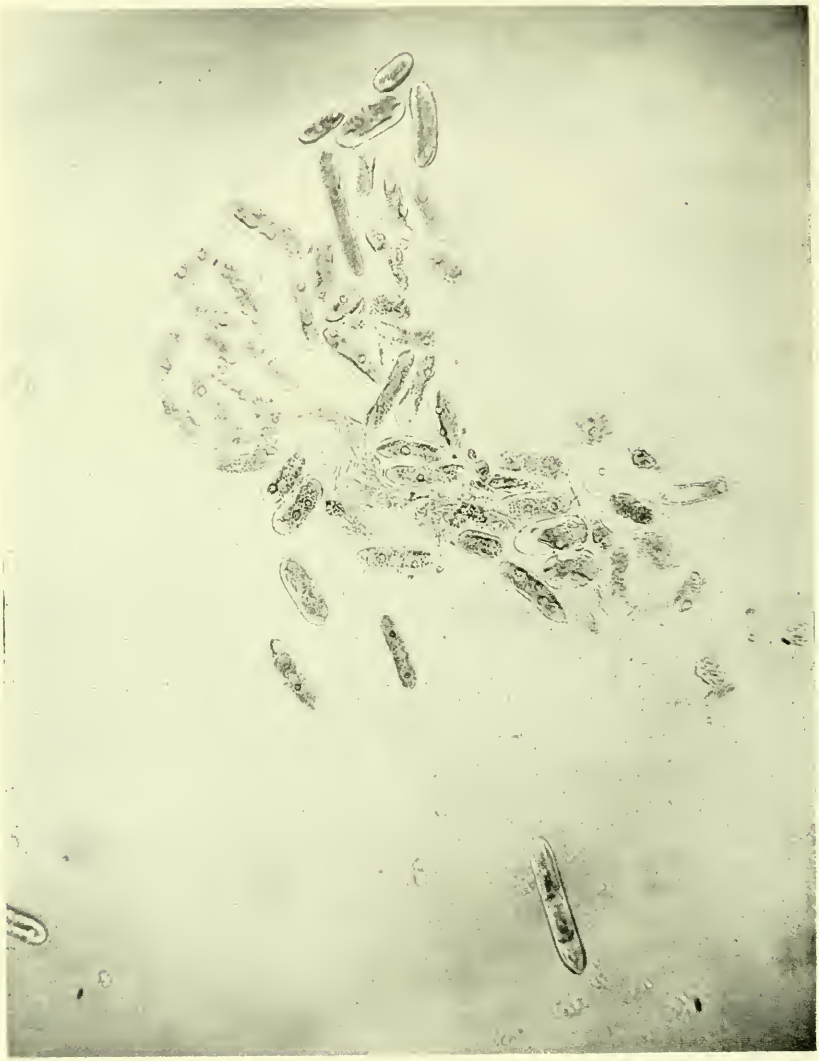


1. WATER BATHS IN WHICH THE FLASKS OF ALGAE ARE IMMERSED

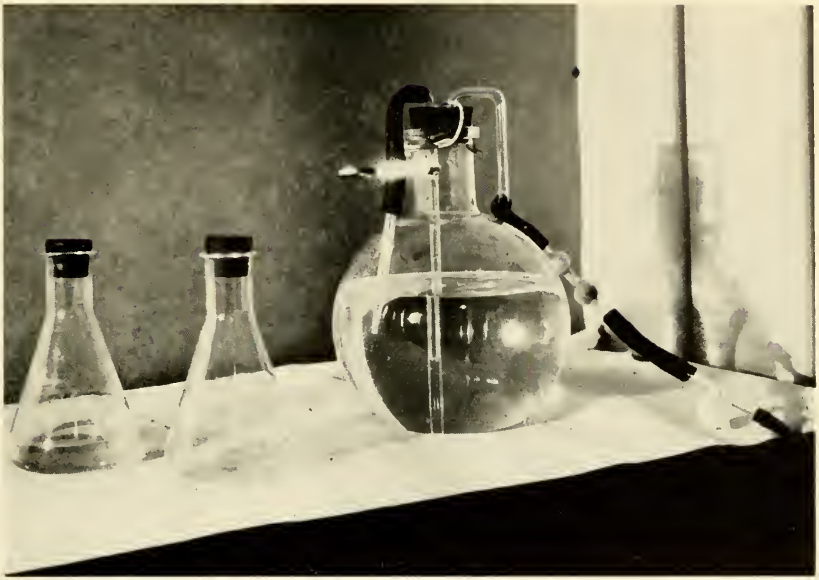
Each flask of algae is enclosed in a container with a light filter on the bottom. Conditions of light, temperature, and humidity are controlled alike in all four baths.



2. NEPHELOMETER EMPLOYED FOR QUANTITATIVE TRANSMISSION MEASUREMENTS TO DETERMINE THE COMPARATIVE AMOUNTS OF GROWTH OF ALGAE

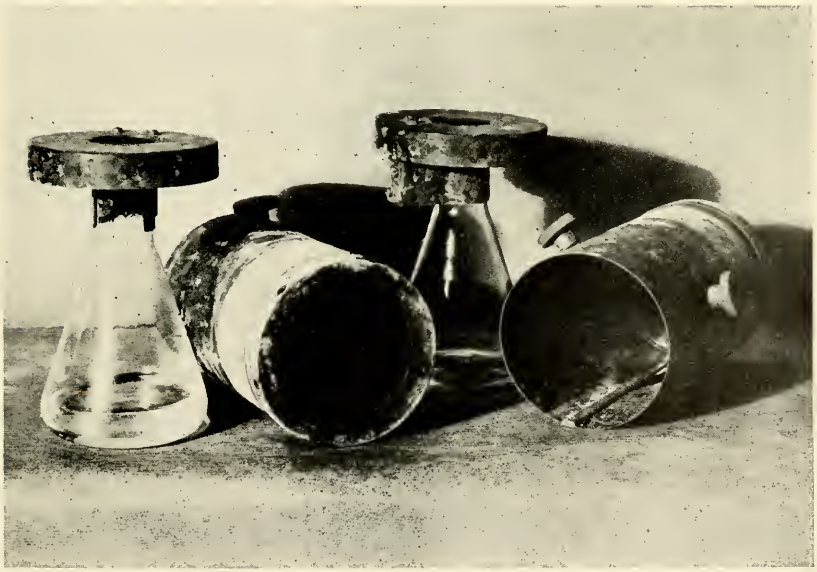


A PHOTOMICROGRAPH OF A TYPICAL DROP FROM A DETMER ⅓ CULTURE OF STICHOCOCCUS BACILLARIS NAEGELI THAT HAS BEEN GROWING IN A NORTH WINDOW FOR ONE MONTH. X 250



1. FLASK IN WHICH THE CULTURE MEDIUM FOR ALL THE CULTURES WAS STERILIZED AND INOCULATED

The sterilized pipette was adjusted to the large container immediately before the culture was poured into the small Erlenmeyer flasks.



2. TWO CULTURE FLASKS READY TO BE INSERTED IN THE METAL CONTAINERS, EACH OF WHICH HAS A DIFFERENT COLOR FILTER ON THE BOTTOM