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Growth Rates of Photosynthetic Microorganisms in Laboratory Cultures

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With 5 Figures in the Text

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A large variety of culture media has been described for the growth of photosynthetic microorganisms in the laboratory. Exact data on growth rates, however, are relatively scarce. Moreover, papers containing such information do not always reveal this by their title.

Since it appeared desirable to obtain quantitative information about growth characteristics of algal strains used in our laboratory, we determined growth rates of our organisms under various conditions and, when possible, compared our results with data given by other authors.

This paper also includes a survey of growth rates of photosynthetic microorganisms reported in the literature. As far as we know no such summary has been published since MYERS' review (1953).

Culture technique

The organisms used in our experiments were cultured in glass vessels closely resembling those described by KOCH (1953) except that they were closed by means of aluminium caps, and that the side tubes for gas supply constituted fixed parts of the vessels instead of being attached by rubber tubings. The diameter of the main compartment was about 35 mm, its height 31 cm. Usually the vessels contained about 150 ml of liquid culture medium. Up to seven of the vessels were placed in thermostated perspex water baths filled with distilled water. The temperature in the vessels was constant within $\pm$ 0.3° C. The baths were placed in wooden boxes, painted white inside, and equipped with tubings for supply of gas and of cooling water. The water baths remained free of algal growth, perhaps because of an inhibitory effect of the copper cooling tubings or because algae are unable to adhere to the perspex surface. The culture vessels were fixed to the rear wall of the boxes by means of clips. The whole set-up is shown in Fig. 1.

The culture vessels were illuminated by banks of 1—5 Philips TL 20 W/32 "warm-white" fluorescent tubes. These banks could be replaced by tungsten lamps if desired. Unless otherwise stated the algae were gassed with a mixture of dry air and 4.5—5.5% CO_2. It was found that evaporation was negligible below 40° C; at higher temperatures a small correction was made. Cotton plugs in the upper parts of the inlet tubes intercepted contaminations. The flow rate of the gas mixture usually was 15—30 ml/min and could be regulated for each vessel separately by means of a needle valve. For some organisms (*Porphyridium, Navicula*) it was neces-

sary to prevent sedimentation on the bottom of the vessels either by using flat-bottomed vessels equipped with a magnetic stirrer or by leading a strong stream of gas through vessels with a conical bottom. The gassing was started as soon as the cultures were placed in the water bath after inoculation. Growth lags, which were observed with many organisms, may at least partly have been caused by this procedure. Cultures for which growth data are reported in this article were always inoculated from liquid mother cultures. As far as we could ascertain, growth occurred under aseptical conditions.

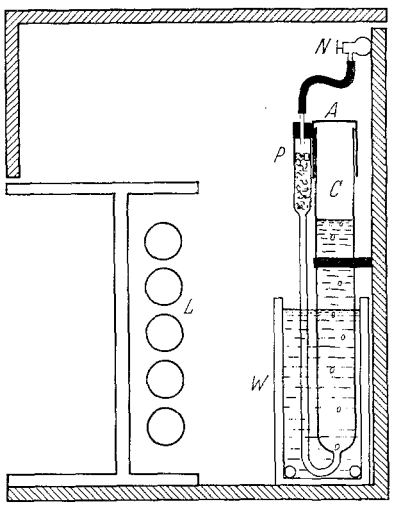

Fig. 1. Culture apparatus. *C* culture vessel; *A* aluminium cap; *P* cotton plug; *N* needle valve; *W* water bath; *L* fluorescent lamps. Further details are given in the text

Since, by reflections inside the box, the culture vessels received illumination from all directions, the light intensities were measured by means of a cylindrical lux meter. This consisted of a photo-resistor (Philips ORP 30, from which the glass bulb had been removed) mounted horizontally in a translucent white perspex cylinder of 30 mm diameter. To approximate the actual illumination conditions at the place of the cells the bottom and top of the cylinder were blacked. It could be immersed in the perspex water bath. The meter was calibrated in unidirectional light by means of an AEG type K lux meter.

Measurement of the growth constant *K*

An exponentially growing culture is defined as one for which the following equation applies: $dN/dt = k \cdot N$, where k is a constant, t is the time, and N is the number of cells or any quantity proportional to this, as e.g. the amount of dry mass or of a certain cell constituent per unit volume. After integration one obtains:

$$k = \frac{{}^{e}\log N_2/N_1}{t_2 - t_1} = \frac{0.69 \cdot {}^{2}\log N_2/N_1}{t_2 - t_1} = \frac{2.30 \cdot {}^{10}\log N_2/N_1}{t_2 - t_1} \quad \ldots\ldots \quad (1)$$

The growth rates of exponentially growing cultures have been reported in the literature in various ways: as "^{e}log units per hour" (K_1), or per day (K_2); as "^{10}log units per day" (K_3), "^{2}log units per day" (= "doublings per day", K), or as the "doubling time in hours" (T_1), or in days (T_2). Throughout this paper growth rates will be expressed in K, the number of doublings per day.

From equation (1) it is seen that:

$$K = K_1 \cdot 24/0.69 = K_2/0.69 = K_3 \cdot 2.30/0.69 = 24/T_1 = 1/T_2$$

Growth was measured by determining the absorbancy at 680 mμ in 10 mm cuvettes in a Zeiss PMQ II spectrophotometer of samples taken aseptically from the

cultures. Opal glass was placed behind the sample and reference cuvettes in order to minimize scattering effects (SHIBATA 1958). A correction for scattering was made by subtracting the measured absorbancy at 740 mμ where no plant pigments absorb.

It has often been discussed whether the absorbancy gives a reliable measure for the number of cells in a suspension. Since Beer's law applies for a suspension up to a relatively high concentration (DUYSENS 1956), the absorbancy is proportional to the concentration of the pigment(s) absorbing at the wavelength of measurement. Thus, as long as the average pigment content of the cells remains constant, the absorbancy is proportional to the number of cells per unit volume. During non-exponential growth the average cell properties may vary with time (cf. e.g. GRIFFITHS 1963, and, for synchronously dividing cell populations, NIHEI et al. 1954), so that the shape of the growth curve depends upon the method of measurement. During exponential growth, however, the average cell characteristics may be presumed to remain the same, so that the absorbancy measurements will yield the same K as cell counts or dry weight determinations. The growth constants reported in this paper are based on experiments in which the absorbancy of the algal suspension increased exponentially four- to twentyfold, indicating that the requirements mentioned above were at least approximately met.

Results

With the equipment described above a series of experiments was done in order to test the reliability of the culture technique. Fig. 2 shows a typical growth curve of the blue-green alga *Schizothrix calcicola* demonstrating a duplicate experiment, in which two culture tubes were inoculated with the same number of cells per unit volume. It can be seen that the two experiments yielded nearly identical results. Also with other organisms duplicate cultures usually gave results which corresponded within a few per cent (cf. Fig. 4 for *Cyanidium caldarium*).

There are several indications that the decrease and eventual cessation of growth of *Schizothrix* and other organisms to be mentioned below was, at least at the highest light intensities applied, due mainly to a change in the composition of the medium such as exhaustion of one or more of the components or accumulation of autotoxic excretion products rather than to mutual shading at increasing population densities (cf. MYERS 1953):

1. We estimated that the average intensity of visible light in a culture, which had been grown at optimal conditions and at the highest light intensity applied, and which had reached its maximal density, was more than 30% of the incident intensity for *Vischeria stellata* and *Chlorella pyrenoidosa*, and more than 50% for *Porphyridium aerugineum* and *Navicula minima*.

2. As will be seen below, for *Chlorella ellipsoidea* the final density was widely different for different media (Fig. 5).

3. With *Schizothrix calcicola* we found an about three times lower growth rate upon reinoculation in old medium, from which the cells had been removed by centrifugation after the end of the exponential growth phase. A similar result was obtained with *Chlorella ellipsoidea* in the medium of TAMIYA (see below).

4. Linear growth as reported by MYERS (1953) was only observed in cultures of *Schizothrix calcicola*, *Ankistrodesmus braunii*, and *Anacystis nidulans* for periods of 1—3 days.

Incidentally results were obtained which were not in accordance with the usual ones. In most such cases technical troubles may have been responsible. It should,

however, be kept in mind that also biological (e.g. genetical) factors may cause changes in growth patterns of cultures. Although infections in the cultures often reveal their presence by changing the appearance of the culture, they may stay unnoticed when no microscopic control is effected for some time. There may, moreover, also occur changes in the cultured material itself (KRASSILNIKOV 1963; REUSSER 1963), resulting in unexpected characteristics where apparently nothing has changed.

In the following sections the results obtained in our experiments will be grouped after the organisms studied, which are ranged taxonomically after the phyla following SILVA's scheme (1962). The values of K presented are the average of 3—10 measurements; the standard deviation usually was between ± 5 and $10\,\%$.

Anacystis nidulans (Richt.) Drouet was obtained from Miss Dr. W. TERPSTRA, Physical Laboratory of the State University, Utrecht. It was grown in medium C of KRATZ and MYERS (1955) to which, when $5\,\%$ CO_2 in air was supplied, 0.840 g $NaHCO_3$ per liter was added to compensate for the pH effect of the higher CO_2 pressure. With $0.5\,\%$ CO_2 and about 7,000 lux K was 2.7 doublings per day at 25° C, light probably not being saturating. At 41° C and 15,000 lux K was 4.7. With $5\,\%$ CO_2 K was the same as reported by KRATZ and MYERS (1955): 2.9 at 25° C and 10,000 lux, and 5.7 at 30° C and 13,500 lux. At 41° C, however, K was 3.6 at 15,000 lux. As with $0.5\,\%$ CO_2 this value is much lower than that found by KRATZ and MYERS. Perhaps our strain has partly lost its thermophilic characteristics because of permanent storage of the stock cultures at room temperature.

Schizothrix calcicola (Ag.) Gom., strain *TX 27*, a filamentous blue-green alga, was given by Dr. B. KOK, Baltimore. Dr. F. DROUET, Philadelphia, kindly identified this algal strain known to us only as "*TX 27*" as *Schizothrix calcicola*. The medium in which it was grown was communicated privately and was prepared by dissolving in a final volume of 1,000 ml: $CaCl_2$, 60 mg; $MgSO_4 \cdot 7\,H_2O$, 150 mg; $NaNO_3$, 500 mg; KNO_3, 500 mg; KH_2PO_4, 250 mg; $Fe_2(SO_4)_3$, 0.4 mg; Tris (Sigma 7—9) buffer, 500 mg; 10 ml of a micronutrient solution, which was obtained by dissolving in 1,000 ml: $(NH_4)_6Mo_7O_{24} \cdot H_2O$, 530 mg; $FeCl_3 \cdot 6\,H_2O$, 300 mg; $ZnSO_4 \cdot 7\,H_2O$, 66 mg; $MnCl_2 \cdot 4\,H_2O$, 430 mg; $Co(NO_3)_2 \cdot 6\,H_2O$, 1.5 mg; $CuSO_4 \cdot 5\,H_2O$, 0.47 mg; H_3BO_3, 3.4 g, and ethylene diamine tetraacetic acid disodium salt (Na_2EDTA), 3 g. After autoclaving the pH of the medium was 7.7. A slight turbidity was formed, but vanished upon gassing with air and $5\,\%$ CO_2.

At 25° C and 15,000 lux K was 3.0, at 6,000 lux 2.7, and at 2,000 lux 1.5. At 30° C and 6,500—14,500 lux K was 3.4 (Fig. 2). However, at this temperature the cultures had a rather bleached appearance and sometimes unpredictably died off, except for a few cells which gave rise to a second increase in cell number. Probably only a fraction of the cell population

was able to adapt itself completely. At 25° C the cultures were much more strongly pigmented, while no unexpected dying off was ever observed.

When 800 lux of incandescent light was added to 1,500 lux of fluorescent light, K was 3.0 at 25° C. Incandescent light appears to be utilized more efficiently than fluorescent light.

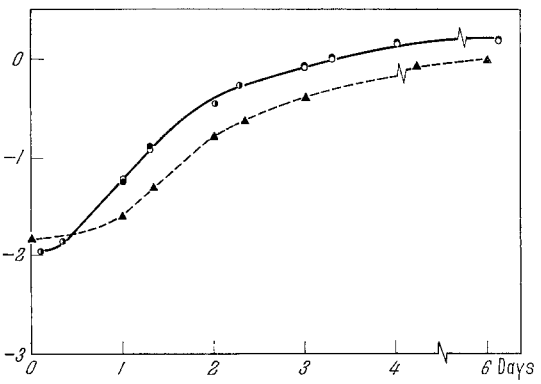

Fig. 2. Growth of *Schizothrix calcicola*; •——• and ○——○ at 30° C and 6,500 lux; ▲——▲ at 25° C and 6,500 lux. The ordinate gives the logarithm of the absorbancy of a 1 cm layer at 680 mμ

Porphyridium aerugineum Geitler, Pringsheim's strain, List nr. *1380/2* of the Culture Collection of Algae and Protozoa at Cambridge, England, was obtained from Dr. E. A. GEORGE. It was grown in a medium originally formulated by PINTNER and PROVASOLI for *Cyanophora paradoxa* (private communication), which had the following composition: $FeCl_3 \cdot 6H_2O$, 1.9 mg; $CaCl_2$, 27.7 mg; $MgSO_4 \cdot 7H_2O$, 100 mg; KCl, 30 mg; ammonium acetate, 200 mg; potassium glycerophosphate, 55 mg; vitamin B_{12}, 1 μg; Tris (Sigma 7—9) buffer, 333 mg; 10 ml of "PII Metal Mix" micronutrient solution; all dissolved in a final volume of 1,000 ml distilled water. The "PII Metal Mix" solution was prepared by dissolving in 100 ml distilled water: H_3BO_3, 114 mg; $MnCl_2 \cdot 4H_2O$, 14.4 mg; $ZnSO_4$, 2.2 mg; $CoCl_2 \cdot 6H_2O$, 0.44 mg; $FeCl_3 \cdot 6H_2O$, 4.8 mg; ethylene diamine tetraacetic acid disodium salt (Na_2EDTA), 100 mg.

At 21° C K was 1.4, independent of light intensity between 3,500 and 15,000 lux (Fig. 3). It was necessary to use a magnetic stirrer to prevent settling down of the cells at the bottom of the vessels.

Cyanidium caldarium Geitler, List nr. *C-14.1.2* of the Laboratory of Comparative Biology of the Kaiser Foundation Research Institute, Richmond, California, was provided by Dr. M. B. ALLEN. It was grown in the medium mentioned in the 1960 edition of the "List of Cultures" of that laboratory. This medium is the same as that given by ALLEN (1959) except that $(NH_4)_2SO_4$ has been replaced by an equal amount of NH_4Cl, and that 0.01 mg Co per liter has been added to the microelements. Data

concerning growth of *Cyanidium* are scarce in the literature. FUKUDA (1958) reports a doubling time as long as about 3.5 days at 45° C and 10,000 lux. ALLEN (1959) states that at 25° C and 6,000 lux *Cyanidium* doubles its weight about daily. Moreover, she claims the optimal temperature for growth of *Cyanidium* to be in the range from 45—50° C.

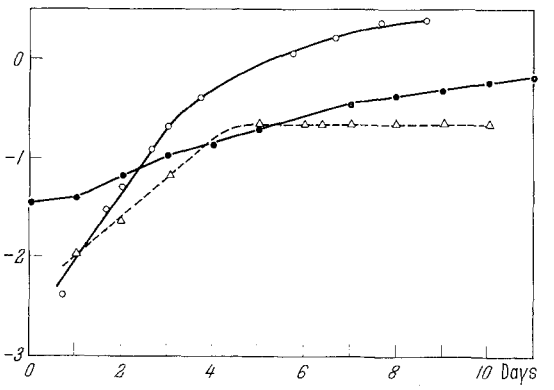

Fig. 3. Growth of *Ankistrodesmus braunii* (o———o) at 22° C and 4,500 lux; of *Vischeria stellata* (•———•) at 25° C and 7,500 lux; and of *Porphyridium aerugineum* (△———△) at 21° C and 3,500 lux. *K*-values of *Vischeria* given in the text were calculated from the first linear parts of the graphs

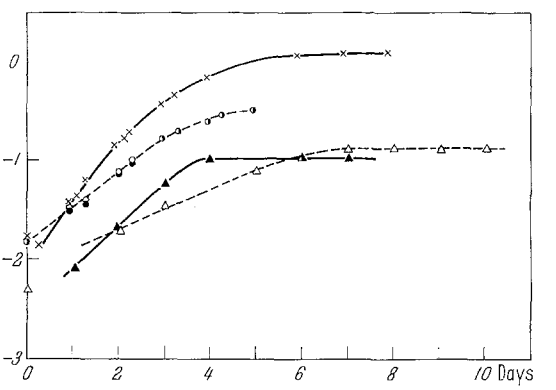

Fig. 4. Growth of *Cyanidium caldarium* at 41° C and 3,300 lux (×———×), at 47.5° C and 2,900 lux (o———o), and at 47.5° C and 5,400 lux (•———•); and of *Navicula minima* at 21° C and 1,700 lux (△———△) and at 25° C and 17,000 lux (▲———▲)

At 47.5° C we found a *K* of 1.3 independent of light intensity in the range of 3,000—9,000 lux; *K* was 2.4 at 39—41° C and 3,000—14,000 lux (Fig. 4). It seems likely that under our conditions the optimum for growth of *Cyanidium* was at temperatures below rather than above 45° C.

Navicula minima Grun., Tanada's strain, was obtained from the Cambridge Collection (List nr. *391*). It was grown in TANADA's (1951) and in VON DENFFER's (1949) media. Both media contain soil extract. The cultures were usually gassed with air

without extra CO_2. A strong stream was blown through vessels with conical bottoms to prevent sedimentation. Preliminary experiments indicated that about the same growth rates were obtained in both media; since VON DENFFER's medium gave a somewhat higher final yield, and since it was much more simple to prepare it was used exclusively for the rest of the experiments.

We found growth rates of about 0.7 at 21°C and 1,700—5,000 lux, and of 1.4 at 25°C in the range of 4,000—17,000 lux (Fig. 4). These values, however, are uncertain because of a large scatter in the experimental results.

Vischeria stellata (Chodat in Poulton) Pascher, received from Dr. TERPSTRA, Utrecht, was grown in a modification of Bristol's medium, communicated by Dr. TERPSTRA and having the following composition: in a final volume of 1,000 ml distilled water were dissolved: $NaNO_3$, 250 mg; NaCl, 25 mg; $CaCl_2$, 25 mg; $MgSO_4 \cdot 7H_2O$, 37.5 mg; K_2HPO_4, 37.5 mg; KH_2PO_4, 87.5 mg; proteose-peptone, 1 g; $FeCl_3$ 1%, 0.1 ml.

At 20°C and 16,000—21,000 lux K was 0.87, though *Vischeria* sometimes failed to grow at this temperature, a phenomenon for which we have no explanation. At 25°C and 5,000—12,000 lux K was 0.70 (Fig. 3).

Ankistrodesmus braunii (Naeg.) Collins, strain Marburg, was supplied by Dr. E. KESSLER, then at Marburg, and grown in the medium of KESSLER et al. (1957). Its growth constant K was 2.3 at 25°C and 12,000 to 14,000 lux. At 22°C and 5,000 lux K was about the same (Fig. 3). This value is much higher than that of CZYGAN (1963) of only 0.45. It was observed that an increase of the inoculated quantum of cells caused a decrease of K, a phenomenon also found by PRATT (1940) for *Chlorella vulgaris* and by OSTERLIND (1949) for *Scenedesmus quadricauda*, but not by VON DENFFER (1949) for *Nitzschia palea*.

Chlorella ellipsoidea Gerneck, strain Japan AOO2 (Tamiya), List nr. *211/1e* of the Culture Collection at Cambridge, England, was cultured in two media given by WATANABE (1960) and indicated MBM (Modified Bristol Medium) and MC (Medium for *Chlorella*) respectively. In both media K was about the same: 3.6 in MBM, 3.4 in MC, at 25°C and 12,000 to 15,000 lux. The final yield, however, measured either as absorbancy or as cell number, was 3—4 times higher in MC than in MBM. Our mean value of 3.5 corresponds very well to that of TAMIYA (1958). Applying Tamiya's medium (HASE et al. 1957) however, also when 1 ml of Arnon's B7 trace element solution was added (cf. TAMIYA et al. 1953), we found a growth constant K of only 2.3 at 25°C and 4,000—13,000 lux. Moreover the final yield was at high light intensities about 20 times lower than in WATANABE's MC medium (Fig. 5).

Chlorella pyrenoidosa Chick, strain Emerson 3, was also obtained from the Cambridge Collection (List nr. *211/8h*). It was grown in the same media as *C. ellipsoidea*. In WATANABE's MBM and MC media K was 2.7 and 3.1 respectively in the range of 25.5—27.5°C and at light intensities of 12,000—15,000 lux. About the same values were found by GALLOWAY

and KRAUSS (1963), by PHILLIPS and MYERS (1954), and by SOROKIN and KRAUSS (1958) for somewhat different media. The highest yield was again obtained in MC medium.

For a number of organisms we tested the constancy of the growth rates with intervals of several months. No indications of changes were obtained.

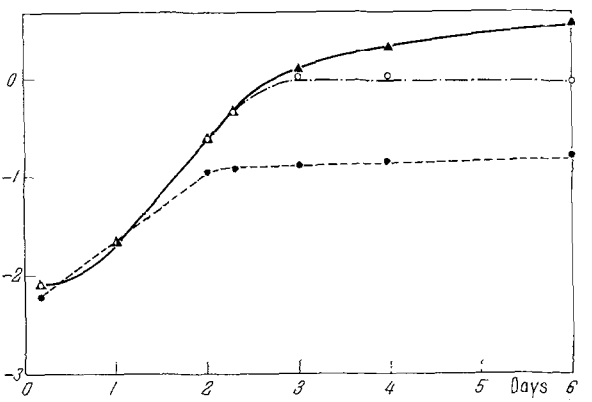

Fig. 5. Growth of *Chlorella ellipsoidea* at 25°C in MC (▲——▲, 15,000 lux), in MBM (○——○, 12,000 lux), and in Tamiya's medium + B 7 (●——●, 13,000 lux)

For *Schizothrix calcicola* at 30°C K values of 3.5 and 3.2 were found with a 2 months interval. K of *Porphyridium aerugineum* at 21°C was 1.3 and 4 months later 1.4. With a 7 months interval K's of 1.3 were found for *Cyanidium caldarium* at 47.5°C. For *Vischeria stellata* a K was found of 0.66 as compared to 0.57 $2^1/_2$ months earlier, both at 25°C. *Chlorella ellipsoidea*, finally, had at 25°C in TAMIYA's medium a K of 2.3, and after 5 months of 2.3 again. All values cited above were obtained at light saturation.

Review of growth rates

The table is a list of growth constants as obtained in the experiments reported above, and as deduced from data presented by other investigators. Such a list may be useful for comparison of results obtained and as a source of information for future culture experiments.

We included in the table the highest growth rates we found for every species listed. For some organisms growth constants reported in other publications were added in order to give some indication about the stability or variability of growth characteristics of the species involved. K values are those given by the authors (recalculated to doublings per day if necessary), or were newly calculated from growth curves presented. In the latter case only curves were used, which showed exponential growth over at least twice the doubling time. Only phototrophically growing organisms have been included, and only continuously illuminated

cultures were taken into account. Thus, synchronized cultures have been omitted. Illumination was assumed to have been continuous if it was not stated otherwise.

Without making an exhaustive search of the literature we included every species of which we found data answering the criteria explained above. The organisms are grouped taxonomically after the phyla.

To the table some additional remarks may be made:

Bacillariophyta. WOOD (1958) claims for *Thalassiosira aestivalis* doubling times of only $^1/_2$ hr., corresponding to a K of 48. However, no data are given concerning the conditions under which this explosive growth took place. A frequently used diatom, *Nitzschia closterium* var. *minutissima*, is listed under its proper name *Phaeodactylum tricornutum* (LEWIN 1958). Some of the literature referred to in LEWIN and GUILLARD's review (1963) was not available to us, so perhaps some data have escaped our attention.

Chrysophyta. Data concerning growth of *Ochromonas malhamensis* (MYERS and GRAHAM 1956) have been omitted regarding the subordinate role phototrophy plays in this alga's nutrition.

Chlorophyta. The highest growth rate reported for *Chlorella pyrenoidosa* is that by CLENDENNING et al. (1956), who obtained a K of 4 in continuous culture. This value, however, is based on the statement that the alga "doubled every 6 hr.", an indication too inaccurate to include this rate in the table. Many more growth rates of *Chlorella* species and strains can be deduced from the data presented by WINOKUR (1948), and by SHRIFT and SPROUL (1963).

As the table shows the high growth rates of photosynthetic bacteria are equalled by some algal species. Apart from WOOD's (1958) scantily documented data for two diatoms, these rates are confined to more or less thermophilic species of the *Cyanophyta* and *Chlorophyta*. Such rapidly multiplying species seem most promising for studies demanding large amounts of cellular material to be produced in a relatively short time span.

In many instances growth rates have been reported in the literature which are considerably lower than those obtained by other investigators with the same species. This not only accentuates the importance of a careful choice of the culturing conditions, but it also demonstrates that a low growth rate, albeit the highest ever reported for a certain species, is not necessarily also the maximal one; it may well be that no optimal medium has been composed as yet. Moreover, apart from the composition of the nutrient solution, also the temperature, CO_2 supply, and light intensity may not have been optimal. With respect to this last factor may be said, that in many publications no indication is given whether the light intensity applied was saturating or not.

Table. *Growth constants of photosynthetic microorganisms, expressed as the number of doublings per day*

Under "Illumination" + means saturating, − non-saturating intensities, and ?: unknown. Under "Medium" s means synthetic, n non-synthetic. Media are classified as non-synthetic when they contained undefined components such as sea water, soil extract, peptone, yeast autolysate etc.

	K	Temperature in °C	Illumination	Medium	Reference
Cyanophyta					
Agmenellum quadriplaticum	8.0	39	?	s	VAN BAALEN and MARLER (1963)
Anabaena cylindrica	0.96	25	+	s	ALLEN and ARNON (1955)
Anabaena variabilis	3.9	34.5	+	s	KRATZ and MYERS (1955)
Anacystis nidulans	11.5	41	+	s	KRATZ and MYERS (1955)
Anacystis nidulans	2.9	25	+	s	KRATZ and MYERS (1955); this paper
Cylindrospermum sphaerica	0.17	25	?	s	VENKATARAMAN (1958)
Gloeotrichia echinulata	0.20	26–27	−	s	ZEHNDER (1963)
Microcystis aeruginosa	1.6	23	?	s	MCLACHLAN and GORHAM (1961)
Nostoc muscorum	3.1	25	?	s	CLENDENNING et al. (1956)
Nostoc muscorum	2.9	32.5	+	s	KRATZ and MYERS (1955)
Schizothrix calcicola	3.4	30	+	s	This paper
Synechococcus lividus	8.5	52	?	s	DYER and GAFFORD (1961)
Synechococcus spec.	9.9	45	?	n	PEARY and CASTENHOLZ (1964)
Synechocystis spec.	8.0	37	?	s	VAN BAALEN (1961)
Tolypothrix tenuis	4.0	38	+	s	UKAI et al. (1958)
Rhodophyta					
Porphyridium aerugineum	1.4	21	+	s	This paper
Porphyridium cruentum	2.5	21	−	s	JONES et al. (1963)
Cryptophyta					
Cyanidium caldarium	2.4	39–41	+	s	This paper
Pyrrophyta					
Gonyaulax polyedra	2.1	21.5	?	n	SWEENEY and HASTINGS (1958)
Gymnodinium splendens	0.92	20	?	n	SWEENEY (1954)
Peridinium spec.	0.90	18	−	n	BARKER (1935)
Prorocentrum gracile	0.83	18	−	n	BARKER (1935)
Prorocentrum micans	0.71	25	−	n	BARKER (1935)
Prorocentrum micans	0.45–0.63	20	+	n	KAIN and FOGG (1960)

Table (Continued)

	K	Temperature in °C	Illumination	Medium	Reference
Bacillariophyta					
Asterionella formosa	2.2—2.4	20?	?	n	LUND (1949)
Asterionella formosa	1.9	18.5	+	n	TALLING (1955)
Asterionella japonica	1.3—1.7	18 & 25	+	n	KAIN and FOGG (1958a)
Cyclotella meneghiniana	0.34	16	?	n	MCLACHLAN (1959)
Cyclotella nana	3.4	20	?	n	GUILLARD and RYTHER (1962)
Detonula confervacea	1.4	10	?	n	GUILLARD and RYTHER (1962)
Navicula minima	1.4	25	+	n	This paper
Navicula pelliculosa	2.0	23	?	s	LEWIN (1957)
Nitzschia closterium	0.49	15	?	s	RYTHER (1954)
Nitzschia palea	2.1	25 or 35	+	n	VON DENFFER (1949)
Phaeodactylum tricornutum	2.7	19	+	n	SPENCER (1954)
Phaeodactylum tricornutum	2.4	8	?	n	UKELES (1961)
Skeletonema costatum	4.3	20 & 30	?	n	CURL and MCLEOD (1961)
Stephanodiscus hantzschii	1.7	20	?	s	SWALE (1963)
Tabellaria flocculosa var. *flocculosa*	1.4	20	+	n	CANNON et al. (1961)
Chrysophyta					
Isochrysis galbana	0.80	20 or 25	?	s	KAIN and FOGG (1958b)
Monochrysis lutheri	1.5	15	?	s	DROOP (1961)
Xanthophyta					
Botrydiopsis intercedens	1.5	25	+	s	BELCHER and MILLER (1960)
Bumilleriopsis brevis	2.9	25	+	s	BELCHER and MILLER (1960)
Monodus subterraneus	0.93	25	+	s	BELCHER and, MILLER (1960)
Polyedriella helvetica	1.1	25	+	s	BELCHER and MILLER (1960)
Tribonema aequale	0.70	25	+	s	BELCHER and MILLER (1960)
Tribonema minus	1.00	25	+	s	BELCHER and MILLER (1960)
Vischeria stellata	0.87	20	+	n	This paper
Euglenophyta					
Euglena gracilis	2.2	25	+	s	COOK (1963)
Euglena gracilis	1.9	25	+	s	CRAMER and MYERS (1952)

Table (Continued)

	K	Temperature in °C	Illumination	Medium	Reference
Euglena gracilis var. *bacillaris*	1.5	25	+	s	CRAMER and MYERS (1952)
Chlorophyta					
Ankistrodesmus braunii	2.3	25	+	s	This paper
Chlamydomonas moewusii	4.2	25	?	s	BERNSTEIN (1964)
Chlamydomonas mundana	11.0	33.4—33.8	?	s	MACIASR and EPPLEY (1963)
Chlamydomonas reinhardtii	3.8	25	+	s	SOROKIN and KRAUSS (1958)
Chlamydomonas reinhardtii	3.3	25	?	s	SAGER and GRANICK (1953)
Chlorella ellipsoidea	3.6	25	+	s	This paper
Chlorella ellipsoidea	3.3	25	+	s	TAMIYA et al. (1958)
Chlorella luteoviridis var. *aureoviridis*	0.56	22.4	?	s	WINOKUR (1948)
Chlorella miniata	0.87	25	?	s	SHRIFT and SPROUL (1963)
Chlorella pyrenoidosa	3.1	25	?	s	GALLOWAY and KRAUSS (1963)
Chlorella pyrenoidosa	3.1	25	+	s	SOROKIN and KRAUSS (1958)
Chlorella pyrenoidosa	3.1	25.5—27.5	+	s	This paper
Chlorella pyrenoidosa	3.0	25	+	s	PHILLIPS and MYERS (1954)
Chlorella pyrenoidosa strain *TX 7-11-05*	9.2	39	?	s	SOROKIN (1960)
Chlorella saccharophila	1.2	25	?	s	SHRIFT and SPROUL (1963)
Chlorella variegata	0.86	25	?	s	SHRIFT and SPROUL (1963)
Chlorella vulgaris	2.9	25	?	s	SHRIFT (1960)
Chlorella vulgaris	2.5	25	+	s	SOROKIN and KRAUSS (1958)
Chlorella vulgaris var. *viridis*	1.6	18	—	s	SHRIFT and SPROUL (1963)
Dunaliella tertiolecta	1.0	16	?	s	MCLACHLAN (1960)
Haematococcus pluvialis	1.2	23	?	s	STROSS (1960)
Nannochloris atomus	0.7—1.3	20	?	s	RYTHER (1954)
Platymonas subcordiformis	1.5	16	?	s	MCLACHLAN (1959)

Table (Continued)

	K	Temperature in °C	Illumination	Medium	Reference
Scenedesmus costulatus var. *chlorelloides*	2.0	24.5	?	s	BRISTOL ROACH (1928)
Scenedesmus obliquus	2.2	25	?	s	WETHERELL (1961)
Scenedesmus obliquus	2.2	25	+	s	SOROKIN and KRAUSS (1958)
Scenedesmus quadricauda	4.1	25	?	s	OSTERLIND (1949)
Selenastrum westii	1.0	25	?	s	VENKATARAMAN and NATARAJAN (1958)
Stichococcus spec.	0.49—0.90	20	?	s	RYTHER (1954)
Schizophyta					
Chloropseudomonas ethylicum	3.3	30	?	s	SYBESMA, unpublished results
Chromatium D	2.6	37	?	s	BENEDICT et al. (1962)
Rhodopseudomonas spheroides	10.1	34	?	s	LASCELLES (1960)
Rhodopseudomonas spheroides	8.5	34	?	s	SISTROM (1963)
Rhodopseudomonas spheroides green mutant	10.8	34	—	s	SISTROM (1962)
Rhodospirillum rubrum	4.5—5.2	25	?	s	ORMEROD et al. (1961)

For algae about 80% of the growth constants lie in the range between 0.5 and 4.0, and 65% even between 1.0 and 4.0. Two doublings a day is a growth rate not achieved by the majority of species listed. In this respect it may be useful to point to the fact that there exists for some species a great difference between doubling and generation times. E.g. after one generation *Chlorella pyrenoidosa* is, under certain conditions, capable of producing as much as 32 autospores (= daughter cells) per mother cell (SENGER 1962). Thus a generation time of 24 hr. corresponds to a doubling time of only 4.8 hr. and a K of 5.0.

Summary

1. Growth rates, measured under various conditions, are reported for *Anacystis nidulans*, *Schizothrix calcicola*, *Porphyridium aerugineum*, *Cyanidium caldarium*, *Navicula minima*, *Vischeria stellata*, *Ankistrodesmus braunii*, *Chlorella ellipsoidea*, and *Chlorella pyrenoidosa* in terms of the growth constant K during exponential growth. A description of the culturing and measuring techniques is given. The reliability of these techniques is discussed.

2. A list of K values is presented, calculated from growth data given in the literature for various photosynthetic microorganisms (algae and bacteria).

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