FUELS FROM SOLAR ENERGY: PHOTOSYNTHETIC
SYSTEMS - STATE OF THE ART AND POTENTIAL
FOR ENERGY PRODUCTION

Final Report

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Abstract

Research on the mass culturing of microalgae has been carried out over the past 30 years in many parts of the world. Today there are numerous potential applications for algal mass cultures including protein production, wastewater treatment, water renovation, closed life-support systems, production of commercial chemicals, aquaculture, and bioconversion of energy. Photosynthetic yields over $30 \text{ gr dry wt m}^{-2} \text{ day}^{-1}$ have been attained on occasion in many locations for short periods and yields between $15\text{--}25 \text{ gr dry wt m}^{-2} \text{ day}^{-1}$ for longer periods are now common. This apparent upper limit in productivity is not coincidental. Under outdoor conditions peak yields are possible only under conditions of light limitation. Photosynthetic algae absorb light energy and convert it to stored chemical energy under rigid adherence to the laws of thermodynamics. By examining the basic physics of photosynthesis, it is possible to clearly demonstrate that under conditions of full sunlight in the most ideal locations maximum yields of $30\text{--}40 \text{ gr m}^{-2} \text{ day}^{-1}$ can be expected. For long-term operation of large-scale outdoor cultures, many bioengineering factors are involved and realistic yields considerably less than the maximum potential can be anticipated. Manipulation of the two independent variables, flow rate and depth, is the key to maximizing yields for varying outdoor sunlight intensities. Future applications for algal mass cultures will probably be restricted to small well-managed systems for solving specific environmental problems in individual communities and not on the grand scale envisaged in the past.

A. Introduction

This study was comprised of three components: 1) a field trip to various laboratories in Europe and Israel where algal mass culturing activities are underway, 2) an intensive literature review on algal mass culturing activities throughout the world over the past 30 years, and 3) a detailed examination of the physics of algal photosynthesis to determine the theoretical upper limit in productivity that is possible under natural outdoor conditions.

A trip report was prepared and submitted earlier on the European-Israeli mass culturing activities (No. COO-4151-1), and appended in this report are two manuscripts dealing with the other topics.

B. Publication Record

- 1977 Goldman, J. C. and Ryther, J. H. Mass production of algae: Bio-engineering aspects. In *Biological Solar Energy Conversion* (Edited by Mitsui, A., Miyachi, S., and San Pietro, A.) pp. 367-378. Academic Press, NY.
- 1978 Goldman, J. C. Outdoor algal mass cultures. I. Applications. *Water Research* (submitted).
- 1978 Goldman, J. C. Outdoor algal mass cultures. II. Photosynthetic yield limitations. *Water Research* (submitted).

INTRODUCTION

For many years, plant physiologists, algologists, and bioengineers have had a special interest in the possibilities of mass culturing microalgae. In the past, the main focus has been on single cell protein (SCP) production (Burlew, 1953; Tamiya, 1957), but in recent years many other potential applications for large-scale algal cultures have been advanced including wastewater treatment, the production of extractable commercial chemicals, closed life-support systems, aquaculture, and the bioconversion of solar energy (Oswald and Golueke, 1968; Oswald, 1969; Ryther *et al.*, 1972; Goldman *et al.*, 1975; Benemann *et al.*, 1977a).

Starting with the basic photosynthetic reaction

and considering that algae require other essential nutrients, particularly nitrogen and phosphorus, in addition to carbon dioxide, water, and light energy, it is possible to envision a multitude of potential algal production systems, as shown in Fig. 1. Although the end products of these processes are distinctly different, they all have a common biochemical and bioengineering basis, that is, the photosynthetic conversion of radiant to bound chemical energy and the transformation of inorganic to organic chemicals through the physical processes of algal growth, separation, and concentration.

It is thus axiomatic that the prime goal of all mass culturing ventures is to maximize photosynthetic conversion efficiencies and produce optimum yields of plant organic material. To achieve this end on a large scale it

is necessary to construct and operate outdoor growth systems to take advantage of available sunlight energy. Although in many respects, the approach is similar to other well-established industrial biochemical processes (e.g. fermentation, yeast production), the fact that algal mass culture systems must be large and exposed to the outdoor environment greatly magnifies the bioengineering problems involved. Specifically, problems relating to culture mixing, nutrient availability and addition, species control, CO₂ addition, water supply and evaporation, and algal separation and harvesting have been of major concern.

Mass culture experiments with microalgae have been carried out with increasing intensity since World War II in many countries. Today, numerous algal wastewater treatment systems are in operation in different parts of the world and a few commercial ventures exist (mostly in Mexico and the Far East) that involve the production of high-priced health foods derived from microalgae (the products are marketed almost exclusively in Japan). Yet, until now the pace of algal mass culture development at the industrial level has been slow and the early dream that SCP could become an important source of protein to offset world-wide shortages, as forecast in the Carnegie Report (Burlew, 1953), certainly has not been realized.

Still the enthusiasm for mass culturing algae has not waned among algologists. Today, the "energy crisis" is providing a dramatic stimulus for renewed interest in the possibilities of achieving both a reliable and constant source of energy through bioconversion, and increased food production through direct harvesting of SCP or by way of aquaculture processes

(Abelson, 1976; Anonymous, 1976; Goldman and Ryther, 1976b; Hall, 1976; Mitsui *et al.*, 1977). Therefore, it is the purpose of this review to examine previous and current work in the field of applied algology with three objectives in mind: 1) to describe the relative merits of existing and new applications, 2) to compare the algal biomass yields attained to date in various geographical locations (and with different species and growth systems) with theoretically possible yields, and 3) to summarize the bioengineering advances and identified constraints associated with mass culture technology. The first objective is the subject of Part I of this review and the remaining two objectives will be addressed in Part II (Goldman, in prep.).

HISTORICAL REVIEW

Early history

Although it is difficult exactly to pinpoint when or where the concept evolved, interest in the mass cultivation of microalgae has grown tremendously over the past 30 years. From an historical perspective, there were several successive scientific breakthroughs which set the stage for the intense mass culture research that originated in the early 1950's and which has progressed steadily over the past several decades.

Before World War II the prime interest of plant physiologists and biochemists was to unravel the mysteries of the photosynthetic process. Algae, particularly the species *Chlorella* and *Scenedesmus* (the hardy and easy to grow green freshwater algae), were the favorite specimens used by these

scientists, primarily because they were unicellular, had reproducible growth characteristics, and could be produced on demand due to their fast reproductive rates. However, laboratory batch cultures were usually restricted to, at best, several hundred milliliter volumes, and frequently there was insufficient algal biomass available for performing all the desired experiments and chemical analyses.

Ketchum and Redfield (1938) devised a simple way to overcome this handicap by exploiting the concept of the "optimum catch," that is, the periodic harvesting of a fixed portion of a population at a crucial point in a batch growth curve; the remaining population would continue to replicate and grow until the desired population was again reached and reharvested. Hence, in this way a semi-continuous supply of algae of a common nutritional and physiological state could be maintained. Ketchum *et al.* (1949) used this technique to grow and optimally harvest cells of several phytoplankton species.

This culture technique was the forerunner of a more automated semi-continuous cultivation system developed by Myers and Clark (1944). Although crude by today's standards, this device was one of the first systems employed for the continuous production of microbes. Simple in design (Fig. 2a), it consisted of five major parts: an illuminated growth chamber, a medium storage bottle, a solenoid valve on a feed line from the medium bottle, a photocell, and a clamped-off withdrawal port. Culture density was maintained at a fixed level by the photocell which controlled the opening of the solenoid valve, thus allowing fresh medium to enter and dilute the culture as required. Samples were withdrawn when desired by manually opening a valve on the discharge

line. The system, not being fully continuous, had the main disadvantage of a varying culture volume and, consequently, it was difficult to maintain a constant cell growth rate.

With the fully continuous culture chamber of Cook (1951) (Fig. 2b) (which was similar in appearance to the culture unit of Myers and Clark) these problems were solved. A withdrawal port at a fixed height in the chamber was used to establish a constant culture volume (10 l), so that medium input and culture overflow were identical. Hence, for a fixed medium flow rate, the dilution rate (fractional volume displacement per unit time) equalled the specific growth rate of the algae once a steady state was reached (i.e., no change in culture biomass with respect to time).

Cook's work at the Stanford Research Institute was part of the first concerted attempt to mass culture algae for potential commercial application. This work was an outgrowth of the earlier studies of Spoehr and Milner (1949), who showed that the chemical composition of *Chlorella*, particularly the fat and protein content, could be readily manipulated by varying growth conditions. Therefore, because protein was relatively expensive and in short supply throughout the world, the concept of mass culturing algae as a food source appeared particularly attractive (Spoehr and Milner, 1949).

Encouraged by the experiments with the small 10 l cultures, Cook's group built a small pilot plant (the first in the United States) consisting of four-570 l growth units (Cook, 1950). Unfortunately, no results were reported and mass culture work at the Research Institute ended in 1950.

Interest in algal mass culturing was continued at that time by the Carnegie

Institution of Washington through a contract with Arthur D. Little, Inc. of Cambridge, Massachusetts. They constructed and ran several pilot plant culture units ranging in size from 700 to 4500 liters during 1951 on the roof of an industrial building (Burlew, 1953). Short-term yields of *Chlorella* were as high as 11 gr dry weight $m^{-2} day^{-1}$, although the average yield for 52 days of operation was only 2 gr $m^{-2} day^{-1}$. It was concluded, however, that yields up to 20-25 gr $m^{-2} day^{-1}$ were possible once culture technology improved and cultivation was performed in more suitable geographical locations. This was a prophetic projection, because almost 30 years later these estimated yields consistently have been reached for short periods, but have not been greatly improved upon.

Following the lead of the Carnegie Institution, interest in mass culturing algae began to blossom in numerous countries including Germany, Japan, and Israel. These international efforts culminated in the now famous Carnegie Report on algal mass culturing (Burlew, 1953) in which the state of the art was updated through 1952. However, most of these early attempts were restricted to short-term studies in very small culture units and yields of the commonly used species *Chlorella* invariably were less than 5 gr $m^{-2} day^{-1}$ (Mituya *et al.*, 1953; von Witsch and Harder, 1953; Milner, 1953). Moreover, the overall goal of these early researchers strictly was to produce protein for potential human and animal consumption, as interest in growing algae for other purposes was not well-developed.

During the period 1955-1970, however, significant advances were made in many areas of mass cultivation technology; small laboratory cultures were

enlarged to relatively large-scale systems, the bioengineering aspects of large-scale culturing were investigated, and the overall objectives were expanded to include the variety of applications already mentioned (Fig. 1). A significant portion of these advances were made in foreign countries, particularly Japan, West Germany, Israel, and France, as well as in the United States.

Recent research

United States: Following the intense research activity sponsored by the Carnegie Institution in the early 1950's, U.S. efforts diminished in the late 1950's because of numerous factors. After the initial successes, it quickly became apparent that the several important advantages of mass algal cultures (i.e., high photosynthetic efficiencies, year-around operation, high plant protein content) were offset by major disadvantages: 1) single-celled algae such as *Chlorella* and *Scenedesmus* were difficult to separate and concentrate and had thick cell walls that made human and animal digestion difficult (Hintz and Heitman, 1965), 2) for commercial food production very large culture systems requiring relatively sophisticated and costly engineering design, construction, and operation were required, and 3) land-based agriculture in the U.S. was highly successful in the 1950's, and there was little interest in, and virtually no need for, single-celled protein.

This pessimism was offset by the enthusiasm of W. J. Oswald and co-workers at the University of California, Berkeley. They revolutionized

the approach to mass algal culture technology in the late 1950's and 60's by demonstrating that large-scale algal cultures simultaneously could be used for protein production and wastewater treatment. The basic scheme involved using domestic wastewater as the nutrient source for freshwater algal growth; the algae in turn produced oxygen for bacterial breakdown of organic matter in the wastewater and, to complete the symbiotic cycle, utilized the carbon dioxide produced by the bacteria (Oswald *et al.*, 1957). The algal-bacterial biomass produced represented a potential source of raw protein, which when harvested, had not only food value, but resulted in a biologically treated wastewater low in BOD and dissolved nutrients such as nitrogen and phosphorus. Oswald's group at Berkeley performed numerous experiments from growing algae on wastewater at the laboratory scale with elaborate continuous culture devices far more sophisticated than Cook's earlier system to small-scale outdoor pilot plant systems (Oswald *et al.*, 1953, 1957; Gotaas and Oswald, 1958). In the early 1960's a 10^6 l capacity ($\sim 2700 \text{ m}^2$ surface area) outdoor mass culture system was put into operation in Richmond, California, with projected algal yields of $12\text{-}18 \text{ gr m}^{-2} \text{ day}^{-1}$ (Oswald, 1969, 1970). This pond was, and still is, the largest outdoor culture system in the U.S. and has a unique design consisting of a series of parallel meandering channels connected in a racetrack type configuration (Fig. 3). Mixing is accomplished by pumping the culture in a recirculating fashion to maintain a desired velocity in the channels.

During this era Oswald's research activities represented the sole U.S. mass culturing effort, and several large scale algal wastewater treatment

ponds were put into operation to serve communities in Northern California. These ponds were modeled to a large extent after the Richmond system (Oswald, 1975), although algal harvesting for protein production was not included in these schemes.

An outgrowth of Oswald's research activities was the demonstration that algal systems had other important functions besides wastewater treatment and protein production. During the mid-1960's interest in bio-regenerative life support systems for possible use in space-craft was great and Oswald and others showed that algal systems could effectively be used in this capacity (Golueke *et al.*, 1959; Oswald *et al.*, 1965; Miller and Ward, 1966; Shelef *et al.*, 1970); however, problems of long-term reliability limited their application and the scheme gave way to the more dependable physical-chemical systems used in the Apollo Moon Program during the late 1960's - early 1970's.

During this same period, Oswald and co-workers demonstrated that algae could be fermented to methane with conversion efficiencies of 50-70% (Golueke *et al.*, 1957; Golueke and Oswald, 1959). Based on these results, they conceptualized a scheme (Fig. 4) whereby the bioconversion of solar to chemical energy could be achieved with algal systems through the fermentation of the algal biomass to methane (Oswald and Golueke, 1960; Golueke and Oswald, 1963). The concept of bioconversion of solar energy through algal mass culturing was not really a new idea at that time, as Burlew (1953) in the preface to the Carnegie Report suggested that energy stored in mass cultured algal cells was greater than the energy required in growing and harvesting the plants.

Similarly, Meier (1955) considered the potential for producing energy from algal biomass either through fermentation or direct combustion. The main attraction of these schemes was that materials were conserved by recycling, while photosynthetic conversion of radiant energy was achieved.

Between 1967-1969 a major research program to investigate the feasibility of removing nitrate-nitrogen from agricultural tile drainage in the San Joaquin Valley of Central California by various biological techniques (including mass culturing and harvesting freshwater algae) was conducted jointly by several State of California and U.S. Government agencies (Price, 1969). The research facilities included a 1000 m² algal pond similar in design to Oswald's system, and 22 small "mini" ponds, each 2.6 m² in surface area. Yields of *Scenedesmus* over 30 gr m⁻² day⁻¹ for short (10 day) periods and average long-term yields of ~10 gr m⁻² day⁻¹ (70 days) were achieved in the large pond (Beck *et al.*, 1969). The high yields were attained by supplementing the drainage water with phosphorus, iron, and carbon dioxide, forcing light to become growth limiting (Brown, 1971). As part of this study, a plan was envisaged whereby 7 x 10⁶ m² of land area in the San Joaquin Valley, originally designated as a storage reservoir, would be converted into a modular algal pond system to treat the entire estimated 1.1 x 10⁹ g day⁻¹ of tile drainage (Goldman *et al.*, 1969). This system would have been the largest mass culture system in the world, but the plan was never realized.

Through the 1960's all U.S. mass culture research had been restricted to growing freshwater algae. In 1971 J. H. Ryther at the Woods Hole Oceanographic Institution in Woods Hole, Massachusetts started work on a marine

counterpart to Oswald's freshwater system. The overall objective was to channel nutrients in wastewater through a marine food chain (Ryther *et al.*, 1972). The first step in the scheme involved mass culturing marine phytoplankton on wastewater-seawater mixtures and then feeding the algal cultures directly to shellfish, thus avoiding the need for the algal separation and concentration steps required with the freshwater culture systems. The shell fish could then be easily harvested and represented an important food source. Experiments with continuous cultures ranged in scope from small laboratory studies to screen marine species for their ability to grow on wastewater-seawater mixtures (Goldman and Stanley, 1974), to small-scale outdoor experiments in two-2000 l (4 m² surface area) circular ponds (Fig. 5a) both in Woods Hole, Massachusetts and Fort Pierce, Florida (Goldman *et al.*, 1974; Goldman and Ryther, 1975; Goldman *et al.*, 1975), and on to large scale outdoor experiments in six-35,000 l (150 m²) ponds (Fig. 5b) at Woods Hole (Goldman and Ryther, 1976a; D'Elia *et al.*, 1977). Yields in long-term experiments (6-18 months) in which several marine diatom species were the dominant algae, ranged from 12-23 gr m⁻² day⁻¹ in the small experimental ponds that were intensively mixed to 6-10 gr m⁻² day⁻¹ in the larger units. These large ponds were each 15 m² square and 1 m deep and consisted of an earthen and sand base covered with a plastic liner. Gentle mixing in each pond was accomplished by recirculation with two small pumps. The simplicity in design was a departure from the more sophisticated design of Oswald's, and yields were less than those achieved in the smaller more intensively mixed ponds, suggesting that in very large systems

mixing problems could result in greatly reduced algal production.

Similar experiments were conducted in 1972-76 by O. A. Roels of Lamont-Doherty Geological Observatory of Columbia University in St. Croix, Virgin Islands. Deep ocean water was artificially upwelled from 870 meters to grow marine phytoplankton in two-45,000 l and six-2,000 l (2.4 m^2) rectangular concrete-lined ponds (Roels *et al.*, 1976). Because the upwelled water contained only 30-35 $\mu\text{g-atom l}^{-1}$ of inorganic nitrogen, productivity could never be made light limiting, and hence dry wt. yields in short-term experiments (<40 days) never exceeded $\sim 10 \text{ gr m}^{-2} \text{ day}^{-1}$. In addition, serious problems were encountered in trying to maintain continuous cultures for more than ~ 6 week periods.

More recently, Oswald at Berkeley carried out mass culture experiments with freshwater bluegreen algae. These organisms, because of their filamentous structure, were considerably easier to separate than the unicellular green algae which typically dominate in outdoor mass cultures. The main thrust of the work was geared towards developing the technology for species control in large systems so that the slower growing blue greens could out compete the faster growing green algae (Benemann *et al.*, 1977a). One technique tried, the continuous recycling of a portion of easily harvested blue-green algae, was only moderately successful. To date, the problem of species control in large-scale outdoor cultures has not been solved adequately.

Japan: Japanese interest in algal mass culturing dates back to the post World War II era, and more than likely stems from the Southeast Asian tradition of using natural seaweeds for human consumption (Tamiya, 1959).

Without question, the early Japanese effort, particularly the research conducted at the Tokergawa Institute for Biological Research and the Institute of Applied Microbiology, University of Tokyo, on the bioengineering aspects of large-scale *Chlorella* culturing is exemplary.

In the first outdoor experiments, conducted during the winter of 1953 in concrete-lined 15 m² troughs, yields were only 3.5 gr m⁻² day⁻¹ (Mituya *et al.*, 1953). Within several years, however, average summer yields were up to 16-17 gr m⁻² day⁻¹ and peak production was as high as 28 gr m⁻² day⁻¹ for several periods (Morimura *et al.*, 1955). A major emphasis in the early Japanese research was on optimizing pond configurations and mixing capabilities. Two basic designs evolved out of this work: the outdoor "bubbling culture" (Morimura *et al.*, 1955), which consisted of long troughs either flat-bottomed (Fig. 6a) or zig-zagged-bottomed (Fig. 6b) in which aeration pipes for bubbling in CO₂-enriched air were placed longitudinally in the troughs, and the "open circulation" method (Kanazaura *et al.*, 1958) consisting of a circular shallow tank with two radial arms on a center support by which the pond culture was circulated when the contents were pumped through small spigots in the arms, causing a jet-type rotating action (Fig. 6c). Watanabe *et al.* (1959) used the "open bubbling" system to mass culture nitrogen-fixing blue-green with the ultimate goal of using the harvested algae as a fertilizer in rice fields. Yields of 6.4 gr m⁻² day⁻¹ in 5 m² culture units were attained.

During the late 1950's a 3200 m² *Chlorella* plant, consisting of a

number of ponds (the largest - 314 m^2 - based on the design in Fig. 6C) was put into operation by the Japan Nutrition Association. This plant was probably the largest culturing unit in the world at that time, and was for the expressed purpose of testing the concept on an industrial scale (Tamiya, 1959). In addition, the Microalgae Research Institute at Kunitachimachi, a suburb of Tokyo, was formed during this period with government and private industrial backing, with a total outdoor culture facility of over 4000 m^2 . Peak average monthly yields were over $4 \text{ gr m}^{-2} \text{ day}^{-1}$ during summer months, but decreased to under $1 \text{ gr m}^{-2} \text{ day}^{-1}$ during the winter (Krauss, 1962).

During the 1960's the emphasis in algal mass culturing switched from the research to the commercial level as a large health food market for *Chlorella* was developed in Japan. Hence, much of the later Japanese research in this area became proprietary and little information is available on this work. As of 1976 it was estimated that the yearly production of *Chlorella* in Japan, involving 10 commercial companies, was over 350 tons. Yearly average production values varied from 8.5 to $21 \text{ gr m}^{-2} \text{ day}^{-1}$ (Tsukada *et al.*, 1977). This high production is caused by the addition of organic sources such as acetate and glucose so that mixotrophic growth occurs. Thus, the cost of producing this biomass is exorbitantly high, ca. \$5-11 per kg. Although *Chlorella* cannot compete with more conventional sources of protein in Japan, its current retail price in health food stores is \$100 per kg, so that a highly profitable, but limited industry exists.

Taiwan: Mass outdoor cultures appear to be used extensively in Taiwan for the commercial production of *Chlorella*. It was estimated that ~800 tons

were produced in 1976 and exported to Japan for sale as a health food (Tsukada *et al.*, 1977). Reported average yields are as high as $22 \text{ gr m}^{-2} \text{ day}^{-1}$ in culture units comprising a total area of $16,200 \text{ m}^2$; each pond is apparently modeled to a large extent after the Japanese open culture technique. In 1977 a massive *Chlorella* plant, comprising a total of $180,000 \text{ m}^2$ of culture ponds, some as large as 500 m^2 , and each made of concrete and fashioned to some degree after Oswald's meandering channel design, was constructed and put into operation (Shurtleff, pers. comm.). Unfortunately, as in Japan, virtually all the mass culture operations in Taiwan are proprietary and little detailed information is available.

Germany: German interest in algal mass culturing dates back to World War II, when experiments were carried out to determine if fat production from algae was possible (Harder and von Witsch, 1942a, b). Mass culture work with *Chlorella* was continued after the war in small-scale outdoor and greenhouse systems (Gumment *et al.*, 1953) and with *Scenedesmus* grown on wastewater (Meffert, 1958).

It was not until research began at the Kohlenbiologische Forschungsstation at Dortmund in the mid-1950's, however, that German interest in algal mass culturing became serious. Work has been carried on continuously since then in a very elaborate and sophisticated outdoor research facility, consisting of four- 80 m^2 ponds, each formed in a raceway type shape with paddle wheels for mixing (Fig. 7). In addition, two- 200 m^2 circular ponds, similar in design to the Japanese open circulation system shown in Fig. 6C,

were used in the earlier experiments. The main objectives of the research were to develop the technology for mass culturing algae for protein production. The cultures were grown on defined artificial media and average yields of the freshwater green algae *Scenedesmus* and *Coelastrum* were typically $10 \text{ gr m}^{-2} \text{ day}^{-1}$ and as high as $30 \text{ gr m}^{-2} \text{ day}^{-1}$ for short periods during summer months in a geographical location not particularly well-suited for mass culturing (Stengel, 1970; Stengel and Soeder, 1975; Soeder, 1976).

Because Germany is a poor location for year-around mass culturing of algae, the Dortmund group, in cooperation with several foreign governments, set up algal research stations in Thailand, Peru and India. The research station in Bangkok, Thailand was particularly elaborate, consisting of seven- 87 m^2 and three- 25 m^2 raceway-type ponds similar to the Dortmund ponds. Reported peak short-term yields were as high as $35 \text{ gr m}^{-2} \text{ day}^{-1}$ for *Scenedesmus* and $20 \text{ gr m}^{-2} \text{ day}^{-1}$ for *Spirulina*, although scant technical data are available (Soeder, 1976).

Czechoslovakia: Mass culture work was begun in 1960 when the Laboratory for Algal Culture was established in Trebon as part of the Institute of Microbiology, Czechoslovak Academy of Sciences. In a radical departure from mass culture pond design of that era (i.e., the Japanese and U.S. designs), the Czechs attempted to maximize algal yields by developing thin, extremely well mixed, culture systems that were designed for efficient utilization of available solar radiation and turbulent mixing.

The first unit built in 1960 was a tilted platform, 12 m^2 in total surface area, comprised of a series of troughs, each slightly elevated

above the other. The algal culture was continually recirculated to the highest trough from the lowest by pumping so that the culture cascaded by gravity essentially in a thin sheet of liquid down the troughs.

Studies with *Scenedesmus* were carried out during 1960-62 with these units in two locations, Trebon and Kosice, and average summer yields were as high as $15 \text{ gr m}^{-2} \text{ day}^{-1}$ (Necas and Lhotsky, 1967).

By the end of 1963, two- 50 m^2 units and one- 900 m^2 unit were constructed, employing the same concept of a tilted surface, in this case made of glass sheets, with baffles for strong mixing, also made of glass. These units were operated during the Spring-Fall between 1963 and 1970. In addition, the 50 m^2 units were operated in Tylicz, Poland in 1966 and in Rupite, Rumania in 1968. Yields varied between $16 \text{ gr m}^{-2} \text{ day}^{-1}$ (average) to $25 \text{ gr m}^{-2} \text{ day}^{-1}$ (maximum) in the 50 m^2 units in Trebon and $22 \text{ gr m}^{-2} \text{ day}^{-1}$ (average) to $30 \text{ gr m}^{-2} \text{ day}^{-1}$ (maximum) in Rupite (Vendlova, 1969). Yields in the 900 m^2 units in Trebon were somewhat lower: $12 \text{ gr m}^{-2} \text{ day}^{-1}$ (average) to $17 \text{ gr m}^{-2} \text{ day}^{-1}$ (maximum), indicating as in the Woods Hole studies, that in a given location yields tend to decrease as the size of the culture unit increases.

Setlik *et al.* (1970) designed a 4500 m^2 version of the cascading system, but the unit was never built. Virtually no information beyond that found in the Laboratory's 1970 Annual Report (Necas and Lhotsky, 1973) is available and it is reported (Soeder, pers. comm.) that mass culture activity in Czechoslovakia is now at a standstill.

Israel: Israeli interest in algal mass culturing began in the early 1950's when A. M. Mayer and his group at the Hebrew University conducted, first

small-scale outdoor experiments with *Chlorella* grown in flasks (Evenari *et al.*, 1953), and then experiments with a 2000 l deep tank having a transparent side facing the sun for better light absorption (Mayer *et al.*, 1958, 1964). Considerable effort was directed at maximizing CO₂ addition, mixing, and light utilization, and yields varied from short-term highs of over 20 gr m⁻² day⁻¹ to average yields of ~10 gr m⁻² day⁻¹.

These studies using artificial media were abandoned in the mid-1960's and no further mass culture work was attempted in Israel until G. Shelef, then also at the Hebrew University, built a 300 m² outdoor pond in Jerusalem, modeled after Oswald's design, and carried out experiments with wastewater-grown algae (Shelef *et al.*, 1973). The main objective of the research was to treat raw wastewater for the removal of organics and nutrients. Summer yields of up to 60 gr m⁻² day⁻¹ of organic matter were reported, but no attempt was made to separate out the non-algal organics that were present in the raw wastewater. However, Shelef made the first attempt to optimize production by showing that there is a bell-shaped response in yield to varying dilution (or flow) rate. Hence, he showed that there is a specific range of dilution rates for which yield is a maximum.

Shelef continued his mass culture work at the Technion, Israel Institute of Technology, under a grant from the German government and in close collaboration with the Dortmund algal laboratory. Two other mass culture projects in Israel were also funded by the German government at that time: one an investigation of certain microbiological and bioengineering problems which was conducted at the Hebrew University, and the other an attempt to

mass culture the blue-green alga *Spirulina* on subsurface brackish water in the desert of southern Israel and performed at the Institute for Desert Research.

Shelef's group at the Technion, carrying out the major effort, focused on using wastewater as a nutrient source for algal mass culturing with three concurrent objectives in mind: wastewater treatment, single-celled protein production, and water reclamation for irrigation purposes. The outdoor experimental station at the Technion consisted of 30 110 l "miniponds" (0.34 m^2 in area and 35 cm deep), six 200 ponds (0.9 m^2 in area and 23 cm deep), and two large ponds, one 120 m^2 in area and the other 150 m^2 . In addition, two $1,000 \text{ m}^2$ ponds have been in operation at Kibbutz Yagur, one of the largest collective farms in Israel. All the ponds were designed in a configuration of meandering channels, similar to Oswald's basic design, and were fed raw wastewater (Fig. 8).

Algal yields over $35 \text{ gr dry wt m}^{-2} \text{ day}^{-1}$ were attained during summer months in both the miniponds and the larger Technion ponds for several dominating freshwater green algae (Shelef *et al.*, 1978). The research emphasis was geared towards the bioengineering aspects of algal growth such as types and degree of mixing, pond design, aeration, etc.

Two large scale algal-waste treatment facilities are currently in operation in Israel. The Dan Region system, below Tel Aviv, consists of a series of 14 conventional oxidation ponds comprising a total area of 134 hectares ($1.34 \times 10^6 \text{ m}^2$), which treats the wastewater from a large section of greater Tel Aviv. In the future, a portion of the system may be converted to high

rate algal ponds, similar to the ones operated at the Technion. In addition, the City of Eilat, on the Gulf of Eilat is serviced by a 20 hectare high rate pond system (Shelef, pers. comm.).

Algal mass culture research began in the Spring of 1974 at the Beer-sheva campus of the Institute for Desert Research and experiments as of 1976 were restricted to six-1 m² miniponds in which algal yields of 10-15 gr dry wt m⁻² day⁻¹ were attained (Richmond, 1976). The research program was later moved to the Sede Boqer campus in the Negev where two 100 m² ponds are used in outdoor experiments. The ponds have a raceway-type shape, broken at one end where the culture is pumped from one pond to the other with the aid of air lift pumps. A portion of this liquid represents the overflow and is passed over gravity-type screen filters for algal separation. The ponds are dirt filled and covered with plastic liners.

A novel new approach to algal mass culturing, conducted by the Israel Oceanographic & Limnological Research LTD., and funded by private industry, involves mass culturing the marine unicellular green alga *Dunaliella* in salt brines up to 5 M concentration. At very high salt concentrations the glycerol content of the organism increases (up to 85 percent of the dry weight) to maintain an osmotic balance. Laboratory and small scale outdoor experiments have been encouraging (Ben Amotz, 1977), and two large-scale ponds similar in design to the Desert Institute's ponds have been constructed in the southern Negev near Eilat to test the concept on a larger scale. Because the project is being funded by industry, the work now being carried out is proprietary.

France: French efforts at algal mass culturing have been restricted to the work of the French Petroleum Institute, which for years has been conducting research on a blue-green alga *Spirulina* (Clement, 1975a, b). This species, which grows abundantly in many African rift lakes high in bicarbonate and other salts and traditionally has been a source of raw protein to the natives in these regions, is of special interest because it has an unusually high protein content (up to 70%), a wide array of pigments which have use as coloring agents, is easily digested by animals and humans, and does not appear to build up toxic chemicals.

Currently, the Institute is collaborating with several countries on *Spirulina* mass culturing (Clement, pers. comm.). In Algeria at Oran and in southern France at Antibes small culture units between 5 and 700 m² in surface area have been constructed. The design is one developed by the Institute (Fig. 9), and consists of two horizontal and adjacent channels, 10-20 cm in depth connected to deeper interconnecting troughs at each end. Carbon dioxide mixtures are introduced at diagonally opposing troughs so that the gas flow causes liquid to be lifted up to the channel where it flows by gravity to the opposing trough and then back again in the adjacent channel. Circulation and CO₂ addition are continuous with the main energy input being the gas addition. The channels are plastic-lined and the troughs are made of concrete.

In addition to these operating systems, several other systems are being constructed or are in early stages of operation: a 2000 m² system in Cairo, Egypt, a 5000 m² unit on an island off of Taiwan (in collaboration with the

Japanese), and a 100 m² system in Martinique in the West Indies. All of these systems are geared towards the production of pigments extracted from *Spirulina* for use as coloring agents.

Along with these studies, the French Petroleum Institute has collaborated with Sosa Texcoco, S. A. of Mexico in developing a *Spirulina* mass culture industry adjacent to Lake Texcoco, near Mexico City, where, because of a unique set of environmental conditions, a natural population of *Spirulina* sp. grows. A 3200 meter diameter solar evaporation lake (850 hectares) is used to concentrate alkaline brines pumped from the water table so that soda ash and caustic soda can be extracted and processed (Fig. 10). In the outer ring of this lake a virtual monoculture of *Spirulina* grows about 10 months out of the year. In 1967 a harvesting and processing plant was built, and nitrate fertilizer was added to about a 20 hectare area (the other essential nutrients are supplied with the concentrated brine) to promote increased productivity. Currently, about two tons dry weight day⁻¹ of *Spirulina* are harvested and dried through centrifugation and drum drying. This corresponds to an areal production of about 10 gr dry wt m⁻² day⁻¹. By 1978 50 hectares will be harvested, leading to a five ton day⁻¹ production level. A new plant is under construction to handle this increased production. Currently, the entire two tons day⁻¹ of *Spirulina* are sold to the Japanese at \$5 per kilogram, and are used for coloring chickens, eggs, tropical fish and other products (Durand-Chastel, 1977).

The culture ponds themselves are primitive by current standards, being about 1 meter deep with virtually no mixing. Improved pond design could

probably lead to much higher productivity. It is important to stress that this system is unique because of the chemical environment developed by the solar evaporation process and could not be readily duplicated in very many other areas of the world.

USSR: Reports in English of Russian activities on algal mass culturing are very scant; however, based upon two available reviews (Gromov, 1968; Dodge, 1976), mass culturing activities in the USSR seem to be extensive, to the point where commercial applications such as the feeding of *Chlorella* to livestock and poultry are practiced. Reported yields of *Chlorella* in outdoor culture systems (sizes unknown) were between $10-20 \text{ gr m}^{-2} \text{ day}^{-1}$ in the earliest studies in Leningrad during summer months (Gromov, 1968). Other mass culture facilities were located near Moscow at the Viliams Institute, in Middle Asia, and in Tadjikistan. Average yields during April-October in a $10,000 \text{ m}^2$ pond were estimated to be $\sim 15-25 \text{ gr m}^{-2} \text{ day}^{-1}$ (Dodge, 1976), although it was not clear as to whether this was a hypothetical estimate or was based on real data in an existing facility.

Gromov and Pinevich (1972) did report data on the cultivation of the blue-green algae *Anabaena variabilis* and *Spirulina platensis* in their Leningrad outdoor facility. With artificially increased temperatures (up to 35°C), yields in July varied from $4.3 - 7.0 \text{ gr m}^{-2} \text{ day}^{-1}$ for *Anabaena* to $9.1-20.0 \text{ gr m}^{-2} \text{ day}^{-1}$ for *Spirulina*.

Netherlands and Belgium: Small scale outdoor experiments in 1 m^2 concrete tanks were conducted in 1951 in Wageningen, the Netherlands, and average

Spring-Fall yields of *Chlorella* were $7.2 \text{ gr m}^{-2} \text{ day}^{-1}$ (Wassink *et al.*, 1953), although peak yields of $13 \text{ gr m}^{-2} \text{ day}^{-1}$ were achieved for short periods during June-July (van Oorschot, 1955). Little additional work has been carried out in the Netherlands with the exception of Wesselius' (1973) studies with small-scale systems to examine the effects of external factors such as light, temperature, and mixing on the productivity of *Scenedesmus*.

Mass culture work in Belgium was initiated recently with efforts focused on the growth of freshwater and marine algae on swine waste (DePauw *et al.*, 1976; DePauw and DeLeenheer, 1977). Summer yields up to $20 \text{ gr dry wt m}^{-2} \text{ day}^{-1}$ in 250 l outdoor cultures were achieved.

ACHIEVED YIELDS

There has been a steady increase in average algal yields achieved during the past 30 years. As seen in Table 1, from the modest beginnings in 1951 of Arthur D. Little Inc. on the roof of a building in Cambridge, Massachusetts where average yields were $2 \text{ gr dry wt m}^{-2} \text{ day}^{-1}$, the mass cultivation of microalgae has spread to virtually all corners of the world. Average yields of $15\text{--}25 \text{ gr dry wt m}^{-2} \text{ day}^{-1}$ are now common.

However, in analyzing the data summarized in Table 1, three important observations come to light. First, the maximum attained yields, regardless of location, algal species grown, and culture system used, are $\sim 30\text{--}40 \text{ gr dry wt m}^{-2} \text{ day}^{-1}$. This apparent upper limit attained by numerous researchers is not coincidental. As shown by van Oorschot (1955), Ryther (1959), and

Shelef *et al.* (1968), limitations in photosynthetic conversion efficiencies are severe under natural sunlight, resulting primarily from the combined effects of limitations in the quantum yield and the light saturation phenomenon common to all plants. The result is that under the most ideal conditions of high sunlight intensity, photosynthetic conversion efficiencies of microalgae are at best ~5% of total available sunlight intensity (Wassink, 1959). Factors further reducing yield potentials include reflective losses of sunlight, algal respiratory losses, daily and seasonal fluctuations in sunlight intensity, and inherent biological uncertainties in maintaining long-term algal cultures. The net result is that, whereas short-term (<30 day) yields over $30 \text{ gr m}^{-2} \text{ day}^{-1}$ have been attained on occasion (usually during summer months), longer-term yields have been considerably lower (Table 1), reflecting the influence of the above factors. The influence of sunlight intensity on algal yields will be discussed in detail in Part II of this review.

The second important observation from Table 1 is that with the exception of the Mexican *Spirulina* ponds of $200,000 \text{ m}^2$ and the *Chlorella* plant on Taiwan totalling $180,000 \text{ m}^2$, most of the yield data for microalgae have been obtained in relatively small outdoor research facilities. Virtually no information is available on the scaling-up problems that might be encountered in constructing and operating very large intensive algal culture systems that might be required for bioconversion plants (Goldman and Ryther, 1977). The Mexican plant is a unique facility, not reproducible in other areas of the world, and the Far East commercial ventures are

elaborate and expensive systems that are geared towards a specific commercial application of limited size and high economic return.

The third observation from Table 1 is that the vast majority of the growth systems used were operated in a semi-continuous mode, that is, the periodic introduction of new medium and the concomitant removal of biomass. The only fully-continuous experiments were those conducted by the Woods Hole and Technion groups (Goldman *et al.*, 1975; D'Elia *et al.*, 1978; Shelef *et al.*, 1978). For particular applications where the flow of incoming water is continuous such as in algal-wastewater treatment systems, continuous growth and harvesting must be practiced. Therefore, the high yields attained in many of the studies shown in Table 1 may not be realistic because they do not reflect potential culturing difficulties that are common with continuous cultures operated for extended periods.

In summary, a major uncertainty in our ability to choose realistic yield values for design and feasibility analyses of large-scale systems is both the lack of available long-term yield data and our inability to forecast the engineering problems that might be encountered with proposed algal systems larger than those reported in Table 1 (Ashare *et al.*, 1978).

CURRENT STATUS AND FUTURE APPLICATIONS

Bioconversion of solar energy

The impact of the "energy crisis" has resulted in a thorough reevaluation of the possibilities for harnessing solar energy (Donovan and Woodward, 1972). Bioconversion through the photosynthetic process has appeal to the

layman because it is the most basic of energy storing processes and because it is responsible for much of the available energy on earth (Anonymous, 1976). In a simplistic analysis it can be considered to be an inexhaustible energy source, and the cost for the raw material is zero. However, as Myers (1977) points out, these two attractions are offset by the fact that radiant energy strikes the earth at a very low flux, resulting in the need for massive and sophisticated collection systems.

It has been estimated that to supply 5% of the projected U.S. energy demand in 1990 via bioconversion with algal mass culturing (as depicted in Figs. 1 and 4) would require land ranging from that equivalent to portions of New England up to an area the size of Texas, depending on the efficiency of the process (Goldman and Ryther, 1977). In addition, staggering quantities of water, nitrogen, and phosphorus would be required (e.g., the combined flows of the five largest rivers in the world). Ashare *et al.* (1978) estimate that it would require an area of over one-half million hectares ($2,000 \text{ mi}^2$) to produce energy through algal mass culturing that would be equivalent to the projected capacity of one large coal gasification plant. Moreover, there is some doubt as to whether a net production of energy with algal systems is even possible (Goldman and Ryther, 1977). These factors, coupled with the uncertainties in scaling up algal systems to the sizes that might be required in bioconversion schemes, reinforce the pessimistic view that solar energy conversion with microalgae has little to offer as even a partial solution to national and world-wide energy needs.

Production of extractable chemicals

The technology for both growing particular algal species and manipulating their chemical composition for the expressed purpose of producing desired chemical products is not well developed. One of the major disappointments of algal mass culturing has been an inability to control algal speciation in outdoor cultures, except in unique chemical environments such as the Texcoco *Spirulina* culture in Mexico City or the Israeli *Dunalliella* project (Goldman and Ryther, 1976a, Oswald *et al.*, 1978). The large size and openness of outdoor algal systems makes it virtually impossible to inoculate with, and maintain a desired species in culture for extended periods. Weed organisms with high growth rates such as *Chlorella*, *Scenedesmus*, and *Microcystis* in freshwater cultures and *Phaeodactylum* and *Skeletonema* in marine systems often become dominant regardless of attempts to exclude them (Goldman and Ryther, 1976a; Benemann *et al.*, 1977a).

Alteration of the nutrient medium to increase the production of a particular chemical in the total biomass, with rare exceptions, has not been successful. This is because the chemical composition of healthy, non-nutrient limited algal cells is typically about 50% protein, 25% carbohydrate, 15% lipid, 5% fiber, and 5% ash (Oswald *et al.* 1978), and high biomass yields in outdoor cultures only can be attained with light-limited and healthy cells. Thus, any manipulation of the chemical medium to alter the chemical composition of the cells, such as forcing increased lipid production through severe nitrogen limitation (Spoehr and Milner,

1949), will lead to low productivity and unstable culture conditions (Richardson *et al.*, 1969).

The most promising approach to maintaining cultures of particular species is to cultivate those organisms that can tolerate extreme environmental conditions and thereby avoid competition with other less versatile species. *Spirulina* and *Dunaliella*, for the reasons cited earlier, are good examples of species that can be grown in unique chemical environments. Unfortunately, such environments rarely occur in nature and are expensive to recreate in mass cultures.

Although the technology for developing a chemical industry based upon algal derivatives is in an infant stage, the possibilities for such an application in the future cannot be discounted. This is particularly true because the cost of producing by conventional means many chemicals that potentially can be derived from microalgae undoubtedly will increase in the future.

Single-celled protein

Traditionally, the main attraction of algae as a protein source has been that they have both a high protein content and a high photosynthetic efficiency, leading to potentially greater yields of protein than most conventional crops. On the negative side, it has been shown that even though the protein content of algae is high, there is an imbalance in the amino acid composition of these proteins, most noticeably in the absence of the sulfur-containing amino acids, methionine and cystine (Waslien, 1975). Hence, the nutritional value of algae is considerably less than conventional

foods such as milk and eggs.

In addition, many of the commonly grown algae, such as *Chlorella* and *Scenedesmus*, have thick cell walls and are not well digested by humans or most animals; thus the cell wall must be ruptured prior to feeding (Waslien, 1975). Another major problem with microalgae is their high nucleic acid content (4% according to Soeder, 1976); hence, when excessive amounts of algae are ingested, unacceptably high levels of uric acid (the decomposition product of nucleic acids) could occur in human blood.

It has been shown in toxicological studies in Germany (Soeder, 1976), France (Clement, 1975b), and the U.S. (Waslien, 1975) that when processed algae is used as a protein supplement in the proper dosages in animal and human diets, there is no evidence of malnutrition, nor any indications of acute toxicity. Unfortunately, most of the above toxicological tests have been of short duration and much longer studies are needed to ensure the safety of eating microalgae (Soeder, 1976).

The main impediments to the development of a microalgae food industry have been consumer non-acceptance and the fact that more conventional protein sources have been in plentiful supply, at least in the western world. In undeveloped and developing nations resistance to eating unconventional foods is not as great and the prospects for obtaining protein supplements from microalgae are more promising. The economics of supplying this type of protein will be the major factor in determining its future role.

Wastewater treatment and water renovation

By far the most successful application of algal mass culturing has been in the field of wastewater treatment. As demonstrated by Oswald (1969; 1973), algal systems have the versatility of not only providing oxygen for BOD removal, but also for incorporating nutrients such as nitrogen and phosphorus into cell tissue, thereby reducing the eutrophication potential in receiving waters. The major drawbacks of these systems are that large tracts of land are required, the process is effective only in areas of high sunlight intensity, and, to avoid regeneration of nutrients in receiving waters, physical separation of the microalgae is required (Benemann *et al.*, 1977a).

Yet, in arid, semi-arid, and tropical climates the use of algal systems in wastewater treatment is becoming widely accepted - e.g., California and the southwest regions of the U.S. (Oswald, 1973; 1975), Israel (Shelef *et al.*, 1978), the Phillipines (Oswald, person. comm.). For example, as mentioned earlier, in Israel algal systems are integrated into a multi-use facility consisting of wastewater treatment, water reclamation for irrigation purposes, and algal biomass production through harvesting. An exhaustive study is currently underway in Israel to determine the feasibility of using wastewater-grown algae as a protein supplement in poultry and fish rations (Shelef *et al.*, 1976; Moraine *et al.* in press; Berk *et al.* in press).

In comparison to conventional wastewater treatment processes such as activated sludge, in locations where the above criteria are met the

algal process (with water reclamation and protein production included) appears to be economically attractive (Moraine *et al.* in press). However, as with using microalgae as a direct human food supplement, the effects of eating poultry and fish that were fed algae previously grown on wastewater, will require long-term testing before the public health risks of the final food products are eliminated.

Another attractive application of algal systems is in treating farm animal wastes such as those from poultry, swine, sheep, and cattle. For example, Dugen *et al.* (1972) developed a novel pilot-scale recycling system for poultry wastes. Chicken wastes were first processed in an anaerobic digester and the digested wastes, in turn, were degraded further in an algal mass culture. The algal biomass was then harvested and used as a feed supplement for the enclosed chickens. In this way, nutrients were continually recycled while at the same time the chicken wastes were effectively treated. The concept should have equal application with other types of farm organic wastes (Oswald *et al.*, 1978).

Aquaculture

Because algae represent the first link in the food chain, they are important food sources for many secondary feeders that have commercial food value. As mentioned earlier, Ryther *et al.* (1975) using wastewater-seawater mixtures, and Roels *et al.* (1976) using upwelled seawater, have attempted to grow various filter-feeding shellfish on mass cultures of marine phytoplankton. Others have grown *Spirulina* on defined artificial media for rearing brine shrimp (Person-LeRuyet, 1976) and freshwater fish

(Stanley and Jones, 1976). In Israel algal feeding experiments with freshwater carp (Shelef *et al.*, 1976, 1978) and marine fish larvae (Ben-Nun, 1976) are being carried out.

The overall prospects for aquaculture will be governed primarily by economic considerations. Where artificial and expensive feeds are used, including algae that were grown on artificial medium, the trend is to produce and market luxury foods such as shrimp, oysters, and clams in order to demonstrate an economic gain (Ryther, 1975). In contrast, the possibilities for recycling waste materials markedly improves the economics of aquaculture, particularly if credits are taken for savings in the cost of wastewater treatment. However, once again public health standards may be difficult to meet. To date, although much progress has been made in developing waste recycling-aquaculture processes (Goldman and Ryther, 1976b), the concept has not gained public acceptance.

SUMMARY

Extensive research has been carried out over the past 30 years in many nations on the outdoor mass culturing of microalgae. Whereas the original interest in this concept was to produce single-celled protein for animal and human consumption, today there are a variety of potential applications including wastewater treatment and water renovation, production of commercial chemicals, aquaculture, and the bioconversion of solar energy. Algal yields up to 30-40 gr dry wt m⁻² day⁻¹ have been reached for short periods in many locations and yields between 15-25 gr

dry wt $m^{-2} day^{-1}$ for longer periods are now common.

Although the "energy crisis" has led to a thorough reexamination of the potential of bioconversion with photosynthetic processes, algal mass culturing on a large-scale does not appear to be a particularly attractive solution, at least in the near future, for both protein production and solar energy conversion. Where the process does appear to have high potential, however, is the fields of wastewater treatment and aquaculture, and as a source of certain chemicals such as glycerol.

Perhaps a major impediment to the progress of algal mass culturing has been that when the concept was first evolved after World War II, it was viewed by many as a panacea to world-wide famine, and was promoted on such a basis. Thirty years later that view has lost much scientific credibility, with the result that progress in algal mass culturing has been retarded, particularly at the research funding level. Yet, from the important recent work of Oswald at Berkeley, Ryther at Woods Hole, and Shalef in Israel, it is clear that algal systems have great versatility for solving environmental problems, particularly when designed as integrated-multi-use systems for wastewater treatment, water renovation, nutrient recycling, and animal protein feeding. In terms of solutions to the "energy crisis," algal systems (if they can be proven to be more energy efficient when used for the above applications) can be viewed as bioenergy "conserving" rather than "converting" processes. The success of this approach will more than likely be realized when algal cultures are applied on a small scale, designed to solve problems on a community by community basis, and not on

the large scale that has been projected in the past.

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Table 1. SUMMARY OF WORLD-WIDE PROGRAMS FOR MASS CULTURING OF MICROALGAE

Year	Location	Species	Culture System		Operation ^a	Best Yields (Duration)				Reference
			Size (m ²)			g dry wt m ⁻² day ⁻¹ (days)				
			Unit	Total		Maximum		Average		
1951	Cambridge, Mass.	<i>Chlorella</i>	56	56	N, F, SC	11	(10)	2	(52)	Burlew (1953)
1951	Essen, Germany	<i>Chlorella</i>	6	6	N, F, SC	?		4	(30)	Gummert et al. (1953)
1953	Tokyo, Japan	<i>Chlorella</i>	15	15	N, F, SC	?		3.5	(10)	Miruya et al. (1953)
1954-55	Tokyo, Japan	<i>Chlorella</i>	2.8- 5.5	13.8	N, F, SC	28	(3)	16	(27)	Horimura et al. (1955)
1957	Tokyo, Japan	<i>Chlorella</i>	7.1- 78.5	147.8	N, F, SC	14	(25)	8.6	(365)	Kamazawa et al. (1958)
1957	Tokyo, Japan	<i>Scenedesmus</i>			N, F, SC	14	(31)			
1958	Tokyo, Japan	<i>Polypothrix</i>	5	5	N, F, SC	?		6.4	(?)	Watanabe et al. (1959)
1958	Tokyo, Japan	<i>Chlorella</i>	314	3,200	N, F, SC	?		?		Tamiya (1959)
1959-60	Plymouth, England	<i>Phaeodactylum</i>	2.6	15.6	N, M, SC			10	(?)	Ansell et al. (1963)
1961	Richmond, California	Green Algae	2700	2,700	W, F, C	?		?		Oswald (1969)
1962	Jerusalem, Israel	<i>Chlorella</i>	4	4	N, F, SC	16	(27)	12	(35)	Mayer et al. (1964)
1960-77	Dortmund, Germany	<i>Scenedesmus</i>	80	320	N, F, SC	28	(?)	10	(?)	Soeder (1976)
1960-62	Trebon, Czechoslovakia	<i>Scenedesmus</i>	12	12	N, F, SC	?		15	(?)	Necas and Lhotsky (1967)
1967	Trebon, Czechoslovakia	<i>Scenedesmus</i>	50	50	N, F, SC	25	(10)	16	(65)	Vendlova (1969)
1966	Trebon, Czechoslovakia	<i>Scenedesmus</i>	900	900	N, F, SC	19	(10)	12	(89)	Vendlova (1969)
1966	Tylitz, Poland	<i>Scenedesmus</i>	50	50	N, F, SC	16	(10)	12	(71)	Vendlova (1969)
1968	Rupite, Romania	<i>Scenedesmus</i>	50	50	N, F, SC	30	(10)	23	(62)	Vendlova (1969)
1969	Firebaugh, California	<i>Scenedesmus</i>	1000	1000	TD, F, C	35	(10)	10	(70)	Beck et al. (1969)
1970-71	Jerusalem, Israel	<i>Chlorella</i>	300	300	W, F, C	60	(30) ^b	27	(30) ^b	Shelef et al. (1973)
1973	Woods Hole, Mass.	Diatoms	4	8	WSW, M, C	13	(15)			Goldman et al. (1975)
1974	Fort Pierce, Florida	Diatoms	4	8	WSW, M, C	25	(15)			Goldman et al. (1975)
1975-76	Woods Hole, Mass.	Diatoms	180	1,080	WSW, M, C	10	(?)			D'Elia et al. (1977)
1967-77	Mexico City, Mexico	<i>Spirulina</i>	?	200,000	B, F, SC	20	(?)	10	(?)	Durand-Chastel (1977)
1976	Haifa, Israel	Green Algae	120	270	W, F, C	35	(30)	15	(365)	Shelef et al. (1978)
1977	Yagur, Israel	Green Algae	1000	2,000	W, F, C	?		?		Shelef (1977)
1974	Bangkok, Thailand	<i>Scenedesmus</i>	87	609	N, F, SC	35	(?)	15	(?)	Soeder (1976)
1974	Bangkok, Thailand	<i>Spirulina</i>	87	609	N, F, SC	18	(?)	15	(?)	Soeder (1976)
1976	Japan	<i>Chlorella</i>	?	11,500	N, F, SC	?		21	(365) ^c	Tsukada et al. (1977)
1976	Taiwan	<i>Chlorella</i>	?	16,200	N, F, SC	?		22	(365) ^c	Tsukada et al. (1977)
1977	Taiwan	<i>Chlorella</i>	250-500	180,000	N, F, SC	35	(?)	18	(365) ^c	Shurtleff (pers. comm.)
1976	Richmond, California	<i>Microcystium</i>	3	12	W, F, SC	12.7	(12)			Benemann et al. (1977b)
1977	Richmond, California	<i>Microcystium</i>	12	48	W, F, SC	32	(30)			Benemann et al. (1978)
1977	Richmond, California	<i>Microcystium</i>	2700	2,700	W, F, SC	11.7	(31)	9.1	(77)	Benemann et al. (1978)

^aN = artificial nutrients; W = wastewater; WSW = wastewater-seawater mixture; B = brine; TD = agricultural tile drainage; F = freshwater algae; M = marine algae; SC = semi-continuous harvest; C = continuous harvest.

^bIncluded non-algal solids from wastewater.

^cAlgae grown on combined CO₂ and organic substrates.

Figure Legends

- Figure 1. Possible applications of algal mass cultures.
- Figure 2. Diagrams of early algal growth chambers: 2(a) modified from Myers and Clark (1944); 2(b) modified from Cook (1951).
- Figure 3. Photograph of 10⁶ liter outdoor algal mass culture system at Richmond, California.
- Figure 4. Schematic diagram of system for the biological conversion of solar energy to electrical power (modified from Oswald and Golueke, 1960).
- Figure 5. Photographs of algal mass culture systems used in Woods Hole, Massachusetts: 5(a) small circular units with strong mixing; 5(b) large ponds with gentle mixing.
- Figure 6. Diagrams of algal culture schemes developed in Japan during 1950's; 6(a) flat-bottomed pond (modified from Morimura *et al.*, 1955); 6(b) Zigzag-bottomed pond (modified from Morimura *et al.*, 1955); 6(c) cross-section of open circulation method (modified from Kanazawa *et al.*, 1958).
- Figure 7. Photograph of algal culture units used in Dortmund, Germany.
- Figure 8. Photograph of 1000 m² algal culture unit located at Kibbutz Yagur, Israel.
- Figure 9. Diagram of the French Petroleum Institute algal pond system (modified from Clement, 1975a).
- Figure 10. Aerial view of solar evaporation pond of Sosa Texcoco S.A. (Mexico) where *Spirulina* is mass cultured.

PHOTOSYNTHETIC REACTION

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5a

Fig. 5b

Fig. 6

Fig. 8

Fig. 9

Fig. 10

APPENDIX B

Outdoor Algal Mass Cultures.

II. Photosynthetic Yield Limitations*

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Abstract:

The photosynthetic conversion of sunlight energy into algal biomass in large-scale outdoor cultures is controlled by the availability of sunlight, the photosynthetic machinery of algae, nutrients, temperature, and the design characteristics of the culture system. For the situation in which light is made the growth rate limiting factor, there is an upper limit in the light conversion efficiency of a large-scale culture, which translates to a maximum potential yield of 30-40 gr dry wt m^2 day under ideal sunlight conditions. In practice, the best yield data for outdoor cultures in various locations in the world has been 30-40 gr dry wt m^{-2} day⁻¹ for short periods and considerably less for longer durations. The development of large-scale mass cultures involves many considerations, but the two major design parameters for optimizing yields at a particular time of year are the flow rate through the culture and the depth.

INTRODUCTION

In Part I of this review (Goldman, in prep.) the historical background and the current status of algal mass culturing throughout the world was presented. It was shown that great strides have been made in the biotechnology of algal mass culturing, and it is now common for yields of 15-25 gr dry wt $m^{-2} day^{-1}$ to be reached for one - three month periods and up to 30 - 40 gr $m^{-2} day^{-1}$ for shorter periods.

As was pointed out in Part I, it is not coincidental that a common upper limit of 30 - 40 gr dry wt $m^{-2} day$ of algal production has been attained in various locations and with a great variety of algal species and growth systems (see Table 1 in Goldman, in prep.). In virtually all the previous outdoor algal mass culture studies a common goal was to optimize biomass yields. To accomplish this end nutrients generally were supplied in excess so that algal growth was regulated by the only two uncontrollable environmental factors, sunlight (intensity and duration) and temperature. Hence, in the many previous outdoor facilities used the upper limit to productivity was controlled by a combination of the radiant energy available from sunlight (which is a function of geographical location and season) and the photosynthetic apparatus of algae (which determines the efficiency by which the available radiant energy is converted to stored chemical energy as organic biomass). Temperature influences the latter process in various ways.

Thus, the objectives of this review are to examine the basic physics and biology of algal photosynthesis and to establish a rationale framework for comparing actual yields attained to date with theoretical yields possible.

This information will be discussed in an overall review of the bioengineering advances made to date in algal mass culture technology.

SUNLIGHT EFFECTS ON ALGAL GROWTH

Algal growth and yield

The kinetics of algal growth basically are similar to bacterial kinetics, with one important difference. Whereas the energy source for bacterial cultures (usually organic carbon) is part of the aqueous medium, for algal growth the radiant energy source is instantaneous and is supplied independent of the growth medium (Fig. 1).

For optimizing algal yields in outdoor mass cultures it is imperative that all nutrients are added in excess so that the light energy incident to the surface of the algal culture is the main yield determinant. As will be demonstrated quantitatively, the key to optimizing the utilization of available light energy is the proper selection of growth rate and depth.

In nature algal growth rates (μ) act as dependent variables, being governed by a multitude of environmental parameters such as light intensity (I), temperature (T), nutrients (S), pH, etc. The response to these parameters are distinctly species specific. Thus,

$$\mu = f(I, T, S, \text{pH, species, etc.}) \quad (1)$$

The specific growth rate of algae is defined as

$$\mu = \frac{\ln 2}{g} = \frac{1}{X} \frac{dX}{dt} \quad (2)$$

in which μ is the specific growth rate [T^{-1}], $\ln 2$ is log to the base e, g is the cell generation period [T], X is the biomass concentration [ML^{-3}], and dX/dt is the change in biomass concentration with respect to time [$ML^{-3} T^{-1}$], or simply the productivity per unit volume. Algal productivity can be normalized on a per unit area basis by considering that for a unit volume V [L^3] of culture with area A and depth d (Fig. 1) the total production of biomass B (XV) [M] per unit time is dB/dt [MT^{-1}]. This latter term can then be divided by the area A [L^2] to give P , the areal yield [$ML^{-2} T^{-1}$]. Thus from equation (2),

$$P = \frac{1}{A} \frac{dX}{dt} V = \frac{1}{A} \frac{dB}{dt} = \mu X d \quad (3)$$

This simple equation is the key to an understanding of how yields can be optimized in outdoor algal cultures. Of the three variables on the right side of equation (3), only X , the biomass concentration, is a true dependent variable. Ideally, outdoor mass cultures should be operated in a continuous flow mode (Fig. 1). Under these conditions a simple mass balance of biomass can be made to relate the increase in biomass per unit time with growth and culture overflow:

biomass change		growth		overflow	
$\frac{dX}{dt} V$	=	μXV	-	FX	(4)

A basic assumption is that the system is a completely mixed-stirred tank reactor so that X is homogeneous throughout the culture volume and is equal to the overflow biomass concentration. Also, only nutrient medium is added to the culture. Then, as long as μ is less than the maximum growth

rate $\hat{\mu}$ of the alga in culture, a steady state concentration of X must be established so that $dX/dt = 0$ (Herbert *et al.*, 1956). By substituting D , the dilution rate $[T^{-1}]$, for FV^{-1} , equation (4) reduces to

$$\mu = D \quad (5)$$

Hence, D , which is the percentage turnover of liquid in the culture per unit time, equals μ at steady state. The flow rate F , which is an independent variable, then controls μ when V is constant. The depth d is also an independent variable, and is equally important as μ in influencing the magnitude of P . Therefore, the main objective of algal mass culturing is the selection of a flow rate-depth combination that will result in an optimum concentration of biomass and resulting yield.

Algal response curves

The response of algal growth rates to variations in the three main environmental factors, nutrients, light intensity, and temperature, can be quantified by examining the shapes of the response curves to each of the parameters with the other two held constant. As shown in Fig. 2(a), when temperature and light intensity are held constant $\mu = f(S)$, where S is a particular limiting nutrient and all other nutrients are supplied in excess. The shape of the curve has been characterized by a rectangular hyperbola for many limiting nutrient situations, but other mathematical relationships have been considered (see Goldman, 1977a). The most important feature of all these curves is that they have the same general shape - they are all first order at low nutrient levels

($\mu = \gamma_S S$) and zero order at high nutrient values ($\mu = \hat{\mu}$) - but diverge somewhat from each other in the transition phase leading from a first to a zero order reaction (Powell, 1972). The value of S for which the extended line from the first-order portion of the curve intersects with the horizontal asymptote describing $\hat{\mu}$ is K_S . For a rectangular hyperbola K_S is the half-saturation coefficient, or the nutrient concentration at which $\mu = 0.5 \hat{\mu}$.

For the situation in which light intensity is variable, but nutrients and temperature are constant, a similar response of growth rate to light occurs [$\mu = f(I)$] [Fig. 2(b)]. Once again, the actual shape of the curve has been debated (Rabinowitch, 1951; van Oorschot, 1955; Shelef *et al.*, 1968), but it has the common feature with the $\mu = f(S)$ curve [Fig. 2(a)] of being first order at low light intensity ($\mu = \gamma_L I$), and zero order at high light intensity ($\mu = \hat{\mu}$). The parameter I_k has the same physical meaning as does K_S . Another important feature of this curve is the value of light intensity (I_S) for which saturation occurs ($\mu = \hat{\mu}$). Depending on the shape of the curve, the relationship between I_k and I_S can be estimated. For example, the form of the equation describing a rectangular hyperbola shape in Fig. 2(b) is:

$$\mu = \hat{\mu} \frac{I}{I_k + I} \quad (6)$$

Because $\hat{\mu}$ is reached only at infinite I ($I_S \rightarrow \infty$), a practical estimate of the ratio $I_S:I_k$ can be made with the approximation that I_S occurs at $\mu = 0.95 \hat{\mu}$. Then rearranging and solving equation (6) $I_S:I_k = 19$. Hence, in this case I_S is substantially greater than I_k .

The influence of temperature on algal growth ratio was examined in detail by Eppley (1972) and Goldman and Carpenter (1974) and it was found empirically from many laboratory studies that Arrhenius-type relationships between $\hat{\mu}$ and T could be demonstrated. For example, the relationship of Goldman and Carpenter was

$$\hat{\mu} = (1.8 \times 10^{10}) e^{-6842/T'} \quad (7)$$

in which T' is the absolute temperature, Kelvin scale, °K. Both the above equation and that of Eppley (1972) generally appeared to be applicable over much of the temperature range that most algae grow (~10-40°C); but for a particular species, depending on its thermal response characteristics, only a portion of the curve was valid. Thus, in Fig. 2(c) only between T₁ and T₃ is the response of $\ln \hat{\mu}$ to T' linear.

A family of curves would then describe the relationships in Figs 2(a) and 2(b) were temperature no longer constant. For algal mass cultures all nutrients would be supplied in excess, so that the effects of both temperature [from Fig. 2(c)] and sunlight intensity on growth rate would be as shown by the curves in Fig. 2(d).

Stored chemical energy in algae

The shape of algal-light response curves determines the efficiency by which radiant energy is converted into stored chemical energy as algal biomass. Considering the basic photosynthetic reaction

the efficiency of photosynthesis (E_T) is simply the rate by which chemical energy is stored in the organic biomass divided by the supply rate of available light energy to drive reaction (8) or

$$E_T = \frac{\Delta H}{\Delta I} \quad (9)$$

The value of ΔH is determined from the heat of combustion (J) of the grown biomass [the biomass in reaction (8) is represented by a basic carbohydrate unit]. However, reaction (8) is a simplified photosynthetic reaction and does not account for both the tremendous potential variation in the chemical composition of algae under different growth conditions and the fact that algae require other nutrients besides CO_2 and H_2O for growth. Numerous researchers have determined the chemical composition of different algae under varying growth and nutrient conditions (Cramer and Myers, 1949; Spoehr and Milner, 1949; Kok, 1952; van Oorschot, 1955). Kok (1952), for example, showed that under conditions of excess NH_3 equation (8) could be expanded to

for growth of the freshwater green alga *Chlorella* and that the biomass produced represented an energy equivalence of 118 k cal mole⁻¹ of CO_2 fixed. On a weight basis this energy content would be equivalent to a heat of combustion of 5.4 k cal gr dry wt⁻¹ of algal biomass, which is within the range of J values (5.2 - 6.3) typically encountered for algae (Oswald, 1957; Shelef *et al.*, 1968). In algal mass cultures under light limitation and

with an excess of nutrients available the carbon:nitrogen ratio typically is ~5-7 by weight (see Goldman and Ryther, 1975, 1976) - values consistent with that shown in equation (10). Hence, numerous researchers (Ryther, 1959; Shelef *et al.*, 1968; Oswald, 1969) have used an average J value of 5.5 k cal gr dry wt⁻¹ in energy balance estimates. If the chemical composition of *Chlorella* in equation (10) is taken as typical for algae grown in mass culture, a J of 5.5 k cal gr⁻¹ would equal 120 k cal mole⁻¹ of biomass. The rate of energy storage in cultured biomass is then

$$\Delta H = JP \quad (11)$$

in which ΔH is the energy stored per unit culture surface area per unit time.

Cell decay and photoinhibition

In contrast to the numerator in equation (9), ΔI , the absorbed chemical energy of photosynthesis per unit surface area per unit time, has been exceedingly difficult to characterize and has been the subject of intense research by plant physiologists for many years (Fogg, 1968; Rabinowitch and Govindjee, 1969). To understand this problem it is instructive to examine the components of the typical light curve [Fig. 2(b)] in detail. Aside from the basic characteristics of the curve described earlier, there are two additional components. First, during photosynthesis and concomitant growth, respiratory and resulting decay processes are at work. Thus, the mass balance equation (4) should be expanded to:

$$\frac{dX}{dt} V = \mu XV - FX - k_d X \quad (12)$$

in which k_d represents a net decay rate [T^{-1}] and is a lumping term to account for all processes leading to a reduction in biomass, e.g. endogenous or dark respiration, photorespiration, cell death, etc. For the steady state situation ($dX/dt = 0$) equation (12) reduces to:

$$\mu - k_d = D \quad (13)$$

so that the dilution rate at steady state is really equal to the net specific growth rate $\mu_N (= \mu - k_d)$.

Just how k_d is affected by environmental conditions (i.e. light intensity, temperature, growth rate) is a much debated subject (Rabinovitch, 1956; Jackson and Volk, 1970; Zelitch, 1971; Tolbert, 1974; Lloyd, 1974; Goldman, 1977a). There is general agreement that dark respiration and photorespiration are mutually exclusive processes in algae (Tolbert, 1974; Lloyd, 1974). At low light intensity dark respiration is relatively more important than photorespiration, but with increasing light and O_2 concentration and decreasing CO_2 concentration the latter process increases and overshadows dark respiration (Jackson and Volk, 1970; Zelitch, 1971). Fogg (1966) has postulated that glycolic acid, the major end product of photorespiration, along with other soluble organic compounds can account for 50 percent or more of photosynthetically assimilated carbon in natural waters; yet, others (Hellebust, 1965; Sharp, 1977) have been unable to find significant dissolved organic carbon levels in algal cultures. The importance of both dark and photorespiration under outdoor mass culture conditions is unknown; but these processes, particularly photorespiration, may be significant because high

light intensity leading to intense algal growth and concomitant high O_2 and low CO_2 levels typically are observed in intense outdoor cultures (Gotaas and Oswald, 1958).

Similarly, although there is little concrete data available on cell decay in outdoor mass cultures, cell death and decay at low growth rates in bacterial cultures seems to be common (Postgate, 1967). Thus, Muller (1972) and Goldman (1977a) suggested that cell decay in algal cultures becomes increasingly important at low growth rates.

Temperature effects on the above decay processes are not well-defined. Both dark and photorespiration appear to increase with increasing temperature, although the relative responses of the two respiratory processes in algae has never been clearly defined (Zelitch, 1971). Thus precisely how k_d is effected in outdoor algal mass cultures is virtually unknown. For lack of a more precise relationship, a common practice in trying to account for decay losses in algal growth models has been to assume a constant value for k_d (Ryther, 1959; Steele, 1966; Tsuchiya, 1966; Shelef *et al.*, 1968), as shown in Fig. 3. The point at which $\mu = k_d$ is commonly referred to as the compensation point (Kok, 1960), and it must be recognized that this value may vary significantly in outdoor cultures depending on environmental conditions.

The second characteristic of the light curve is that at very strong light intensity there is a falling off in photosynthetic activity resulting from light inhibition (Fig. 3). First observed by Myers and Burr (1940) in several freshwater green algae, light inhibition was also shown by Ryther

(1956) for a variety of marine microalgae and by Abellovich and Shilo (1972) and Eloff *et al.* (1976) with freshwater blue-green algae. Rabinovitch (1945) suggested that this inhibition by strong light was simply the result of photooxidative processes. Both Steele (1962) and Ryther (1959) accounted for this phenomenon in developing algal productivity models. Ryther (1956) showed that light saturation for marine green algae, diatoms, and flagellates starts at $\sim 0.07 \text{ cal cm}^{-2} \text{ min}^{-1}$, which is only ~ 10 percent of full sunlight intensity. Therefore, light inhibition in outdoor mass cultures may be an important factor regulating productivity and cannot be ignored in growth models (Platt *et al.*, 1977).

Photosynthetic efficiency

To quantitatively describe the photochemical conversion of radiant energy in algal mass cultures, Shelef *et al.* (1968), following the basic concepts of van Oorschot (1955), wrote the following simple energy balance:

$$P = \frac{E_T}{J} (I_o - I_d) - D_T \quad (14)$$

in which E_T is the overall efficiency of photosynthesis, I_o and I_d are respectively the visible radiant energy incident to the surface and at depth d in a culture in units of energy per surface area per time, and D_T is the overall decay term in gr dry wt per area per time. If algal cultures were optically thin cultures so that there was no self-shading of light, and if the radiant energy source were monochromatic (that is, light energy of a particular wave length), then estimates of P could easily be made. However, as Shelef *et al.* (1968) demonstrated in detail, the actual determination of P is far more complicated

because in mass cultures algal cell densities are high enough so that self-shading is important, and also because E_T and the absorptive characteristics of light vary with wave length. Photosynthetic absorption of sunlight occurs in the visible region (400 - 700 nm) so that the wave length dependency of light utilization by algae must be considered.

The overall efficiency of photosynthesis is a function of the two main phenomena controlling the shape of the light-response curve, the initial slope of the curve ($\gamma_L = \mu I^{-1}$), and the magnitude of I_k and I_s , the parameters describing the light saturation effect. In general terms, the initial steep slope of the light curve in Fig. 3 is controlled by the light reactions of photosynthesis and describes the maximum possible efficiency of the process (Kok, 1960). The tailing off portion describing light saturation is the region where the dark reactions (i.e. the carbon cycle reactions) become rate limiting and set an upper bound to photosynthesis - if the curve remained linear algal growth rates would be directly proportional to light intensity at any light level.

Determination of γ_L has been the subject of exhaustive research among plant physiologists, and to this day the value of γ_L is still a controversial issue (Emerson, 1958; Kok, 1960; Rabinovitch and Govindjee, 1968; Ng and Bassham, 1968).

According to the quantum theory of Planck, and Einstein's application of this theory to photochemistry, it is known that light energy to drive the photosynthetic reaction (8) is used in discrete packets called quanta. Each quantum E on a molecular basis has an energy equivalent

$$E = h\nu = \frac{hc}{\lambda} \quad (15)$$

in which h is Planck's constant (6.62×10^{-27} erg-sec), ν is the frequency of light propagation, sec^{-1} , c is the speed of light propagation, 3.0×10^{10} cm sec^{-1} , and λ is the wave length of light transmission in nm ($= 10^{-7}$ cm). On a molar basis the total light energy U in einsteins is $N_A E$, in which N_A is Avogadro's No. (6.02×10^{23} molecules mole^{-1}). Hence, the total light energy required to drive reaction (8) is $\theta^{-1} U$, in which θ^{-1} is the quantum yield or efficiency in whole integers (θ is commonly referred to as the quantum requirement).

In theory, one einstein of energy has an energy equivalence of ~ 40 - 60 k cal depending on wave-length (Rabinovitch, 1951), so that the minimum quantum yield in photosynthesis would be at least 2-3 since the heat content of plant biomass is ~ 120 k cal mole^{-1} .

In reality, more than 2-3 quanta are needed, although the exact number has been the subject of intense debate (see Rabinovitch, 1951; 1956; Franck, 1953; Emerson, 1958; Kok, 1960). Based on many experimental studies, it is now generally agreed upon that a minimum quantum yield of 8 per mole of CO_2 assimilated (and more typically 10-12) is required in photosynthesis (Rabinovitch and Govindjee, 1968; Kok and Radmer, 1976). Thus, assuming that $\theta^{-1} = 10$ and the heat content of algae is 120 k cal mole^{-1} , then the thermodynamic efficiency [$E_q(\lambda)^*$ - the maximum possible efficiency] of photosynthesis for a given wave length of light is:

$$E_q(\lambda)^* = 0.000412 \lambda \quad (16)$$

As can be seen by the plot of equation (16) in Fig. 4(a), $E_q(\lambda)$ varies linearly from 0.16 at 400 nm to 0.29 at 700 nm.

The above analysis is based on the assumption that the quantum efficiency is independent of wave length and that photosynthesis occurs with equal efficiency throughout the visible light spectrum. This assumption is not true, and, as both Ryther (1959) and Shelef *et al.* (1968) have shown, the thermodynamic efficiency $E_q(\lambda)$ must be corrected for the effect of wave-length. As seen in Fig. 4(b), the relative quantum requirement Q_λ ($= \theta / \theta_{\max}^{-1}$, in which $\theta_{\max}$ is the maximum quantum requirement attained throughout the visible spectrum) for three algal species representing different taxonomic divisions is plotted against wave length. The curves for the green alga, *Chlorella pyrenoidosa*, and the diatom, *Navicula minima*, are remarkably similar; but the curve for the blue-green alga, *Chroococcus*, deviates significantly from the other two below a wave length of ~ 575 nm, although a dip in Q_λ in this wave length region is common to all three species. The carotenoid pigments absorb light in this region, and they are not as efficient in passing absorbed light on to the photosynthetic apparatus, particularly for blue-green algae (Rabinovitch and Govindjee, 1968). At 670 - 680 nm, the region for maximum chlorophyll a absorption (a pigment common to all three taxonomic groups), Q_λ for all species is ~ 1.0 . To demonstrate the weighing effect of Q_λ on $E_q(\lambda)$, the average Q_λ for *C. pyrenoidosa* and *N. minima* from Fig. 4(b) was determined. Then, from the equation

$$E_q(\lambda) = Q_\lambda E_q(\lambda)' \quad (17)$$

$E_q(\lambda)$, the weighted thermodynamic efficiency, was determined as a function of wave length [Fig. 4(c)]. Whereas the average $E_q(\lambda)'$ is 0.23, the effect of Q_λ reduces the average $E(\lambda)$ to 0.20, as determined by graphical integration.

The second consideration in establishing the overall photosynthetic conversion efficiency E_T is determination of the light utilization efficiency E_S , which is a function of the shape of the light response curve (Fig. 3). The earliest attempt to quantitatively account for the effect of light saturation was by Burlew (1953) who presented the equation

$$E_S = \frac{I}{I_0} \left(\ln \frac{I_0}{I_s} + 1 \right) \quad (18)$$

which he attributed to V. Bush. Shelef *et al.* (1968) formally derived equation (18) from the basic relationship

$$E_S = \frac{\text{total applied light} - \text{unutilizable light}}{\text{total light applied}} \quad (19)$$

The above formulation was based on the considerations that 1) light energy is dissipated in a vertical water column containing a concentration X of algae by the Beer-Lambert Law

$$\frac{dI}{dt} = -\alpha X I_d \quad (20)$$

in which α is the extinction coefficient (and is wave-length dependent) and I_d is the light energy remaining at depth d , and 2) that light energy greater than I_s is not utilized. As seen from the graphical representation of equation (18) (Fig. 5), at very low light intensity ($I_0 I_s^{-1} \leq 1$) $E_T = 1.0$ and falls

off, first rapidly between $1 \leq I_0 I_s^{-1} < 20$, and then more gradually when $I_0 I_s^{-1} > 20$. For the condition of $E_q = 0.2$, the overall efficiency E_T can also be determined from Fig. 5.

The value of I_s is then the major factor in determining E_s for outdoor algal mass cultures where I_0 is an independent variable. Clearly, the most ideal situation is to grow an algal species with a high I_s value. Good values of I_s from the literature for different species generally are lacking (Table 1). A major problem in using what data are available is that until recently light intensity generally was measured as illuminance (e.g., ft-candles, lux), and not as total radiant energy (e.g. Wcm^2 , $\text{cal cm}^{-2} \text{min}^{-1}$). Although conversion factors to relate illuminance measurements with particular light sources to equivalent radiant energy units are available (Bickford and Dunn, 1972), they give, at best, a crude approximation of I_s in radiant energy units because of the many factors influencing the spectral qualities of a particular light source. Moreover, much of the I_s data available, as seen in Table 1, are restricted to a few species, most notably *Chlorella pyrenoidosa*, because this alga was a favorite test species of early researchers. Hence, the only value of Table 1 is in establishing the general magnitude of I_s for different classes of algae and in demonstrating the effect of temperature on the efficiency factor.

Ryther (1956) compiled light curves for 14 marine phytoplankton species representing three different taxonomic groups (green algae, diatoms, and dinoflagellates) and found that the light curve for each group was of a distinctly different shape (Table 1). Based on his data and the other data shown in Table 1, it appears that in the temperature range $20^\circ\text{--}25^\circ\text{C}$ I_s values for green algae

(both freshwater and marine) and marine diatoms vary between about 0.02 - 0.06 cal cm⁻² min⁻¹. Marine dinoflagellates have an usually high I_s value (0.125 cal cm⁻² min⁻¹), but are generally difficult to grow in culture and are never dominant species in outdoor mass cultures of marine algae (Goldman and Ryther, 1976; Goldman, 1977b). Therefore, on the basis of their high I_s value dinoflagellates would appear to be good candidates for marine mass cultures, but other factors exclude them from consideration.

The most striking feature of the light saturation effect is that much of natural sunlight is wasted in photosynthesis. This effect can best be seen in Figs. 6(a) and 6(b), in which the effect on E_s of low incident radiation - 0.2 cal cm⁻² min⁻¹ (representing a cloudy day) is compared with high incident radiation - 0.7 cal cm⁻² min⁻¹ (full sunlight) when $I_s = 0.04$ cal cm⁻² min⁻¹. Although light penetration is greater with the high incident light intensity, the relative fraction of light wasted is also greater. Thus, although the total light available for photosynthesis [as represented by the shaded areas of Figs. 6(a) and 6(b)], and the resulting potential yield of biomass, is greater at the higher light, the efficiency of light use is considerably reduced. For the range of I_s values typically observed (0.02 - 0.06 cal cm⁻² min⁻¹) E_s varies from 0.5 - 0.9 at very low light (0.1 cal cm⁻² min⁻¹) down to 0.1 - 0.3 at high light (0.6-0.8 cal cm⁻² min⁻¹) [Fig. 6(c)]. Assuming that E_q is 0.2, then the overall efficiency of photosynthesis E_T is reduced to 0.02 - 0.2, depending on the incident light energy available for photosynthesis and the light saturation intensity of the algal species under cultivation.

SUNLIGHT CHARACTERISTICS

Total sunlight available

Solar energy strikes the earth's outer atmosphere at a rather constant intensity of $1.94 \text{ cal cm}^{-2} \text{ min}^{-1}$ (Thekaekara, 1976). By the time this energy reaches the surface of the earth it has been dissipated considerably by a combination of light scattering and absorption by water vapor, carbon dioxide, ozone, dust particles, and cloud cover within the atmosphere (Strickland, 1958). The angle at which the sun's rays strike the earth (the angle of incidence) influences the magnitude of the above losses, and determines the radiant energy incident to the surface of the earth. This latter effect is controlled by latitude, season, and time of day.

Sunlight intensity reaching the surface of the earth is usually measured with a pyranometer (see Robinson, 1966, Thekaekara, 1977 for reviews on sunlight-measuring techniques). In the U.S. there is a network of 90 stations (Thekaekara, 1977) and in Canada 34 stations (Parsons *et al.*, 1977) reporting solar irradiance measurements to respective government agencies. Gotaas and Oswald (1958), using solar irradiance data compiled by the U.S. Weather Bureau up to 1954, prepared a table of the maximum and minimum expected values for average monthly sunlight intensity (total and visible) in 2° latitude intervals. From these data, summarized in Fig. 7, it is seen that on a monthly basis peak total sunlight intensities vary from $700 \text{ cal cm}^{-2} \text{ day}^{-1}$ at the equator during the spring and fall equinoxes to $780 \text{ cal cm}^{-2} \text{ day}^{-1}$ at latitude 50°N or S in June. At the

higher latitudes in June, even though the sun is not completely perpendicular to the earth, the days are longer than at the equator during the equinoxes, resulting in higher peak intensities.

Monthly variations in average solar irradiance measured with Eppley 6-90 pyranometers (Payne, pers. comm.) are also shown for two locations in the United States: Woods Hole, Massachusetts (lat. $41^{\circ}31'$) and Ft. Pierce, Florida (lat. $27^{\circ}28'$) (Fig. 8). Based on the Woods Hole data for 1975-77, variations in sunlight intensity are quite consistent from year to year and fall within the maximum-minimum expected values tabulated by Gotaas and Oswald (1958). Thekaekara (1976) recently compiled sunlight data obtained from 80 stations in the United States during 1971-74 and prepared a map of average yearly sunlight intensities expected in $50 \text{ cal cm}^{-2} \text{ day}^{-1}$ intervals (Fig. 9). Maximum yearly averages ($>450 \text{ cal cm}^{-2} \text{ day}^{-1}$) occur predominantly in the southwestern portions of the country, with specific peak intensities of $526 \text{ cal cm}^{-2} \text{ day}^{-1}$ in El Paso, Texas, $498 \text{ cal cm}^{-2} \text{ day}^{-1}$ in Albuquerque, New Mexico, and $493 \text{ cal cm}^{-2} \text{ day}^{-1}$ in Tucson, Arizona.

Visible sunlight intensity

Only light in the visible region (400-700 nm) is available for photosynthesis. Recently Goldberg and Klein (1977) and Klein *et al.* (1977) made accurate measurements of the spectral variation in sunlight energy in several locations over a four year period (197-74). They found that the visible portion was consistently in range of 0.40-0.46 of the total available energy, except for days of extreme low intensities ($<50 \text{ cal cm}^{-2}$

day⁻¹) when the visible fraction increased to ~0.50. Previously, Strickland (1958) and Ryther (1959) suggested that a value of 0.5 of total sunlight energy be used to describe the energy available for photosynthesis, recognizing that a number of factors including cloud cover and time of day influence the ratio of visible to total sunlight. However, based on the new data available, an estimate of 0.45 for E_v , the visible fraction of sunlight, appears more reasonable, particularly when considering long-term average intensities.

Spectral variations in sunlight

Variations in the spectral distribution of total sunlight energy have been determined [Fig. 10(a)] and it is apparent that the visible and infrared (>700 nm) portions account for virtually all of the available energy. Based on the maximum light energy at ~490 nm, as seen in Fig. 10(b), the average efficiency factor E_I for the entire visible spectrum is ~0.89, as calculated by graphical integration.

Surface reflection and back scattering

A small portion of sunlight striking a water body is both reflected and back scattered. The magnitude of the loss is a complicated function of many factors, e.g., angle of incidence, wind velocity, cloud cover, turbidity. For an angle of incidence >30° losses on a calm, clear day would be only a few percent, but could increase to >10% for light winds and >30% for moderate to strong winds (Strickland, 1958). Ryther (1959) used an average loss of 5% in his productivity analysis and Strickland (1958) suggested an average 15% loss for use in field estimates. Thus, a

reasonable approximation of the efficiency of light transmission E_R across the air-liquid interface is 0.90.

ALGAL PRODUCTIVITY

Average growth rate and mixing

Light energy is dissipated over the depth of an outdoor culture so that an algal cell at the surface sees considerably more light than a cell at the bottom. Therefore, although equation (12) is valid at steady state, it really describes an average specific growth rate. For an individual cell moving about in a mixed culture, its instantaneous specific growth rate varies depending on its vertical position. Conversely, the average amount of light an individual cell sees in a culture of constant volume V is a function of the flow rate and the concentration of biomass present.

Because in a well-mixed culture cells move about randomly and are intermittently exposed to low and high light intensity, and because the photosynthetic light reactions are orders of magnitude faster than the dark reactions of carbon assimilation (Kamen, 1963), it is valid to integrate over the depth d any productivity equation that incorporates a diminishing light intensity I_d with depth, e.g., $\mu = f(I_d)$ (Shelef *et al.*, 1968). Moreover, as shown by Fredrickson *et al.* (1961), conventional mixing does little to improve the efficiency by which cells moving randomly through a culture can absorb light so as to increase productivity. Similarly, Powell *et al.* (1965) showed mathematically the improbability of increasing

productivity through very intense mixing in order to enhance the "flashing light effect," a biochemical phenomenon by which photosynthetic rates of an algal cell are increased when the cell is transferred back and forth from light to dark in a time sequence corresponding to the light and dark biochemical reactions (Rabinovitch and Govindjee, 1968). However, mixing is required for several other reasons: to prevent settling and subsequent decay of organic matter, to prevent thermal stratification, to break down diffusion gradients of essential nutrients which could develop at the cell surface in intense mass cultures, and to provide uniform cell exposure to light. Mixing can also, to some degree, enhance CO_2 transport from the atmosphere; but, because of the very low concentration of CO_2 in the atmosphere (0.03%), the transport gradient is always small and CO_2 transport is ineffective unless very turbulent mixing is employed.

Vertical light attenuation

As discussed earlier and shown in Figs. 5(a) and 5(b), the vertical attenuation of light in a water column generally has been described by equation (20), or its integrated form

$$I_d = I_o e^{-\alpha X_d} \quad (21)$$

Shelef *et al.* (1968) pointed out that equation (21) is valid only for monochromatic light: for polychromatic light the wave length-dependency of α must be considered. Hence, to properly use equation (21) $\alpha = f(\lambda)$ must be known and integrated over the visible spectrum. Both Shelef *et al.* (1968) and Dabes *et al.* (1970) grew specific algal species with known light sources

and were able to develop relationships for $\alpha = f(\lambda)$ for use in their integrated productivity models. However, in outdoor cultures $\alpha = f(\lambda)$ is extremely difficult to estimate. For natural phytoplankton populations that are usually orders of magnitude more dilute than mass cultures, a common practice has been to assume a constant value for the product αX (usually when X is expressed as chlorophyll concentration) (Bannister, 1974). Just how much accuracy is lost in predictive models by assuming a constant value for αX has never been established. In mass cultures in which X is usually expressed in dry wt and varies considerably, there is little rationale for assuming a constant value of αX .

Models of the light curve

To use equation (3) for determining the optimum yield in a flowing algal mass culture that is light-limited, the function $\mu = f(I)$ must be established. Determination of the true shape of light response curves has been the subject of intense research (see reviews by Rabinovitch, 1956; Patten, 1968; Straskraba, 1976; Platt *et al.*, 1977). As described earlier, the shapes of most curves considered are similar at the extremes of light intensities typically encountered, but diverge somewhat in between. Straskraba (1976) has classified the light curves developed by others as those that incorporate functions to account for photoinhibition at high intensities and those that do not. In reality, it has been virtually impossible to ascribe any physiological meaning to any of the curves developed, and, for the most part, individual researchers have chosen particular shaped curves (described by specific mathematical relationships) purely on empirical grounds, that is, finding the relationship that

best described their data.

For mass cultures, probably the most extensive analyses of various light curves was by van Oorschot (1955) and Shelef *et al.* (1968). van Oorschot (1955) developed the following relationships of $\mu = f(I)$ for three basic saturation-type curves (light inhibition effects were not considered):

1. first order - zero order

$$\mu = E_q I, I_0 \leq I_s = I_k \quad (22)$$

$$\mu = \hat{\mu}, I_d > I_s = I_k$$

2. exponential

$$\mu = \hat{\mu} (1 - e^{-I_d I_k^{-1}}) \quad (23)$$

3. rectangular hyperbola

$$\mu = \hat{\mu} \frac{I_d}{I_k + I_d} \quad (24)$$

Then, using these relationships in equation (3), and considering equation (21) for describing light dissipation through depth d , the final integrated relationships for productivity P as a function of incident light intensity I_0 were:

1. first order - zero order

$$P = \frac{E_q}{J} [I_k (\ln \frac{I_0}{I_k} + 1) - I_0 e^{-\alpha X d}] \quad (25)$$

2. exponential

$$P = \frac{E_q}{J} I_k [\alpha X d + E_1 (\frac{I_0}{I_k}) - E_1 (\frac{I_0}{I_k} e^{-\alpha X d})] \quad (26)$$

in which E_1 represents exponential integrals that can be determined from standard E_1 tables.

3. rectangular hyperbola

$$P = \frac{E_q}{J} I_k \ln \left[\frac{I_k + I_o}{I_k + I_o e^{-\alpha X_d}} \right] \quad (27)$$

Shelef *et al.* (1968), by considering the wave length-dependency of E_q , α , and I_o , developed the fully integrated versions of equations (25)-(27). It was found by experimentally determining the wave length dependency of the above parameters for a given artificial light source, that equation (26) best fit data collected from a light-limited continuous culture of *Chlorella pyrenoidosa*. No consideration was given to light inhibition effects, but cell decay was accounted for by assuming that k_d , as used in equation (12), was 0.125.

In engineering practice the use of light models such as equations (25)-(27) or others may be impractical for designing outdoor mass cultures because of 1) the tremendous uncertainties in choosing proper numerical values for the many coefficients involved, 2) the need to integrate the equations over the visible portion of the light spectrum, and 3) the daily and seasonal variations in sunlight which seriously complicate use of the equations. The equations are very useful, however, in demonstrating the importance of growth rate on algal biomass concentration and resulting yield, and in estimating the maximum potential yield possible in a particular geographical region.

Maximum potential productivity

Considering the various components of the light curve and the characteristics of sunlight it is possible to expand on the simple energy balance of equation (13) to include all the efficiency factors previously discussed. Thus

$$P = \frac{E_q E_s E_R E_I E_V}{J} (I_o' - I_d') - D_r \quad (28)$$

in which I_o' and I_d' are total sunlight intensities incident to the surface and at depth d (as opposed to I_o and I_d which are the visible light intensities). For algal mass cultures it is reasonable to assume that most of the incident light I_o' will be dissipated over the culture depth so that $I_d I_o^{-1} \approx (1 - E_D)$, in which E_D is the efficiency of light dissipation (~0.95). Then equation (28) reduces to:

$$P = \frac{E_q E_s E_R E_I E_V E_D I_o'}{J} - D_r \quad (29)$$

As van Oorschot (1955) and Shelef *et al.* (1968) demonstrated, when E_s is determined from equation (17) and when $I_o \gg I_d$, equation (25) with the various efficiency factors added is identical to equation (29). Because the $P = f(I)$ curve described by equation (25) gives the maximum possible estimate of productivity (Shelef *et al.*, 1968), it is instructive to use this equation to estimate the upper limit of attainable yields in outdoor mass cultures. For convenience, the fully integrated version of equation (29) will not be considered, although it is clearly recognized that this is an oversimplification. Yet, the equation still is useful because consideration

has been given to the weighting effect of wave length by inclusion of the average efficiency factors Q_λ and E_I . In addition, by assuming that E_D is 0.95, the wave-length dependent α is eliminated from the equation. Because the best available information has been used to estimate the various efficiency factors, equation (29) should provide a reasonable estimate of the maximum potential productivity outdoors.

Consequently, by using the previously estimated values for E_q , E_R , E_I , E_V , E_D , and J , and not considering decay, and with equation (18) inserted for E_s , equation (29) reduces to:

$$P = 0.28 I_s \left(\ln \frac{0.45 I_o'}{I_s} + 1 \right) \quad (30)$$

in which P is in gr dry wt $m^{-2} day^{-1}$ and I_s and I_o' are in $cal\ cm^{-2}\ day^{-1}$. Equation (30) is plotted in Fig. 11 for a span of I_s^* ($0.02 - 0.06\ cal\ cm^{-2}\ min^{-1}$) and I_o' ($0-800\ cal\ cm^{-2}\ day^{-1}$) that represent the maximum range of conditions likely to be experienced with outdoor cultures.

The productivity curves clearly resemble the $\mu = f(I)$ curves in shape. Although, a three-fold increase in I_s leads to an approximate doubling in yield at the higher light intensities, the light saturation effect results in a flattening of the curves so that large increases in light intensity lead to small increases in yield. For example, short-term yields during June at high latitudes when total solar radiation is at a peak ($600-780\ cal\ cm^{-2}\ day^{-1}$, Figs. 6 and 7) would not be much greater than average yearly yields in the best of locations such as the southwest regions of the United States, where average yearly intensities are $450-525\ cal\ cm^{-2}\ day^{-1}$ (Fig. 9).

* $I_s = I_k$ when the Bush equation is substituted for E_s in equation (30), and optically dense cultures are considered.

By not considering decay and light inhibition at the highest light intensities, peak yields between ~ 30 - 60 gr dry wt m^{-2} day $^{-1}$ can be expected. However, the effects of these two parameters cannot be ignored even though they are difficult to model. For example, Ryther (1959), by determining $E_s = f(I_o')$ empirically from a composite light-response curve [that included light inhibition effects and was based on data compiled from numerous studies with 14 marine algal species (see Table 1)], and by assuming that $k_d = 0.07 \mu$, was able to construct realistic curves for estimate of maximum productivity under natural sunlight. These curves, with and without decay considered, are plotted in Fig. 11 for comparison with the energy balance curves constructed from equation (30).

The Ryther curves are based on a composite I_s of ~ 0.1 cal cm^{-2} min $^{-1}$, reflecting the influence of the high I_s value for dinoflagellates (Table 1), an I_s value that, as previously discussed, is somewhat unrealistic for mass culture conditions. However, even with the high I_s value, the overall effect of light inhibition on yield is considerable at the higher light intensities. As seen in Fig. 11, the Ryther curve falls between the energy balance curves that were based on lower I_s values, but did not include any factor for light inhibition. With decay considered the Ryther curve is reduced even further so that productivity begins to exceed decay only at $I_o' > 100$ cal cm^{-2} day $^{-1}$ and reaches a maximum level of ~ 30 gr dry wt m^{-2} day $^{-1}$ at the peak light intensities.

Comparisons of actual and theoretical yields

As shown in Table 1 of Part I of this review (Goldman, in prep.), maximum

algal yields attained in a variety of locations and with different species and growth systems consistently have been in the range of 30-40 gr dry wt day⁻¹. Invariably, these studies were carried for relatively short (< one month) durations during periods of high solar radiation at a given location. Based on the productivity curves (Fig. 11), it is not coincidental that 30-40 gr m⁻² day⁻¹ represents an upper limit in achievable productivity. By considering all the factors influencing productivity, Ryther's curves predict a maximum attainable yield of 30-40 gr m⁻² day (Fig. 11) and are consistent with the energy balance curves. In fact, the energy balance curves were based on the most liberal considerations (i.e., the Bush equation, no decay and no light inhibition). The large data pool of maximum yields attained in outdoor systems (Table 1 in Goldman, in prep.) adds strong support to the credibility of the curves in Fig. 11.

In trying to estimate actual yields that might be attained on a long term basis in large scale mass cultures from Fig. 11, a number of factors must be considered. First, the peak yields attained have been achieved only for relatively short periods (<30 days), and longer term yields have been considerably reduced (~10-20 gr m⁻² day⁻¹) (Goldman in prep.). Second, in virtually all the studies to date, the growth systems have been less than ~3000 m² total area. The exceptions are the Mexican *Spirulina* and Japanese *Chlorella* plants that have unique characteristics (Goldman in prep.). Thus projection of attainable yields in a given location must be based, not only on available sunlight, but also on a scaling factor. This factor would summarize numerous effects that generally fall under the category of

inherent biological and bioengineering difficulties in maintaining large scale algal cultures for indefinite periods. Considering these factors, Ashare *et al.* (1978) chose $P = 6 \text{ gr dry wt m}^{-2} \text{ day}^{-1}$ as a design parameter in carrying out a cost analysis of algal bioconversion processes. Choosing a design yield may involve a subjective bias, but it is clear from theoretical considerations and from the field data available, that a reasonable estimate would be a substantial fraction of $30\text{-}40 \text{ gr m}^{-2} \text{ day}^{-1}$.

BIOENGINEERING ASPECTS

Examination of the productivity curve [equation (29)] with decay included ($D_r = k_d Xd$, units of $\text{gr dry wt m}^{-2} \text{ day}^{-1}$) is instructive, not only for estimating peak attainable yields, but also for gaining an appreciation of how manipulation of the net specific growth rate (really flow rate) and the depth are key factors in optimizing yields for seasonal changes in I_0' .

A simple example will illustrate the above point. Consider that the coefficients in equation (29) are all known. Then for a given level of I_0' and depth d , the curve of P vs X will be bell-shaped with a unique concentration of biomass X' corresponding to a peak yield P' when any of the productivity equations (25)-(27) are used in equation (29) [Fig. 12(a)]. In a similar fashion, the curve of P vs μ_N will also be bell-shaped and P' will occur at a unique net growth rate μ_N' [Fig. 12(b)]. Using the information from Figs. 12(a) and 12(b) and equation (3), a plot of decreasing biomass X with increasing growth rate μ_N can then be developed [Fig. 12(c)]. The bell shape of Figs. 12(a) and 12(b) results because: 1) decay is negligible

at high growth rates (low X), but becomes increasingly more important as μ_N decreases (X increases), and 2) as μ_N increases (X decreases) the time each cell is exposed to light decreases with a concomitant decrease in photosynthesis and resulting P . Qualitatively, the peak in the bell shaped curves occurs when the light dissipation efficiency factor E_D is a maximum ($\sim 0.95-1.0$) and cell decay is still relatively unimportant. A family of curves can then be constructed for μ_N' vs I_0' at different depths [Fig. 12(d)]. From this figure, and the following rearrangement of equation (3)

$$\mu_N' d = \frac{P'}{X'} \quad (31)$$

it is clear that any combination of μ_N' and d (at a given I_0') equaling $P'X'^{-1}$ will lead to maximum productivity.

Thus, for year-around operation of an outdoor mass culture, either the flow rate or the depth can be adjusted as I_0' varies in order to establish the conditions for maximum potential productivity, as in Fig. 11.

In reality, curves such as those in Fig. 12(d) may be extremely difficult to establish without an exhaustive research endeavor. Curves with shapes similar to those in Figs. 12(a-c) have been established from light-limited continuous culture studies in the laboratory (Pipes and Koutsoyannis, 1962; Shelef *et al.*, 1968; Dabes *et al.*, 1970), and from outdoor mass culture experiments (Shelef *et al.*, 1973; Goldman and Ryther, 1975; Goldman *et al.*, 1975; D'Elia *et al.*, 1977; Benemann *et al.*, 1977) (Figs. 13 and 14). But, as seen in Fig. 14, μ' and P' vary considerably from one study to the other,

reflecting the many different environmental conditions involved (i.e., location, latitude, culture system, depth, species). Hence, for a given location the choice of μ_N' and d at a particular time of year to give P' will most likely be chosen on a trial and error basis. In certain cases economic considerations (cost of land vs cost of pumping) will control the choice of μ_N and d , and in other situations the flow rate may be fixed, as when the algal system is used as a wastewater treatment system. For the latter use, the dimensions of the system (area and depth) will be the only true independent variables.

SUMMARY

As has been demonstrated in this review, the conversion of solar energy to plant biomass is a rather wasteful process. At best, conversion efficiencies <5 percent of total sunlight can be expected, leading to short-term potential yields of 30-40 gr dry wt $m^{-2} day^{-1}$. Such yields have been attained on occasion, but longer-term yields have been considerably lower.

On a bioengineering basis, the major challenge is to design large-scale outdoor cultures so as to achieve maximum potential yields consistently as a function of available sunlight intensity. To accomplish this end, consideration must be given not only to the independent variables controlling light utilization efficiencies (i.e., flow rate and depth), but also to many other factors affecting algal growth (mixing, nutrient supply, pH control, predator control, etc.). A major uncertainty is if

there exists a negative relationship between the size of an algal culture and the sustained yields possible. Little data are available on this subject, but the best yields to date seem to have been achieved in small, well-managed experimental cultures (Goldman, in prep.). Clearly, much future research on the bioengineering aspects of mass culturing is warranted.

Probably little can be done to improve the actual efficiency of photosynthesis in algal cultures, as has been achieved over the years in conventional land-based agriculture. The major problem is that, whereas species control is relatively simple with terrestrial crops so that the best suited species are grown, virtually all attempts to grow specific algal species outdoors for sustained periods have failed (see Goldman, in prep.). Due to the rapid generation periods of algae, certain species tend to dominate through natural selection regardless of which alga is used as an inoculum. Invariably, the weed species such as *Chlorella*, *Scenedesmus*, and *Microactinium* in freshwater cultures and *Phaeodactylum* and *Skeletonema* in marine systems tend to become dominant over time (Goldman and Ryther, 1976).

One very strong selective force controlling algal speciation in mass cultures is temperature (Goldman and Ryther, 1976). Because temperature strongly influences I_g , it would seem that high outdoor temperatures ($>30^{\circ}\text{C}$) would lead to high yields. However, although algal growth rates are a function of temperature, respiratory and other decay processes are also influenced by this parameter. The net effect is that temperature is not nearly as important as sunlight in controlling productivity (Goldman and Ryther, 1976, Goldman, 1977b).

As discussed in Part I of this review (Goldman, in prep.), the uses of large-scale algal cultures may be restricted to solving specific environmental problems such as wastewater pollution and water renovation. The efficiency of these processes is directly proportional to the biomass of algae grown. The upper limit in yield of 30-40 gr dry wt m⁻² day⁻¹ is clearly an intrinsic characteristic of the photosynthetic process, and will probably never be improved upon very much in large-scale cultures. It is this yield constraint that must be considered in determining the feasibility of any outdoor mass culture venture.

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List of Symbols

- A - culture area, m^2
 B - total biomass, mg
 c - speed of light, 3×10^{10} cm sec $^{-1}$
 d - culture depth, m
 D - dilution rate, day $^{-1}$
 D_r - decay factor, gr dry wt m^{-2} day $^{-1}$
 E - energy per quantum, molecule basis, k cal einstein $^{-1}$
 E_s - light utilization efficiency
 E_q - thermodynamic efficiency
 E_T - total efficiency of photosynthesis
 $E_q(\lambda)'$ - wave-length dependent thermodynamic efficiency
 $E_q(\lambda)$ - wave-length weighted thermodynamic efficiency
 E_D - efficiency of light dissipation
 E_I - sunlight visible region efficiency factor
 E_R - efficiency of light transmission at air-liquid interface
 E_V - visible fraction of total sunlight
 F - flow rate, l day $^{-1}$
 g - cell generation period, day
 h - Planck's constant, 6.62×10^{-27} erg-sec
 ΔH - rate of chemical energy storage in algal biomass, cal cm^{-2} day $^{-1}$
 ΔI - rate of light absorption by algal biomass, cal cm^{-2} day $^{-1}$
 I_0 - total incident light energy at culture surface, cal cm^{-2} day $^{-1}$
 I_0' - visible incident light energy at culture surface, cal cm^{-2} day $^{-1}$

- I_d - incident light intensity at depth d , $\text{cal cm}^{-2} \text{ day}^{-1}$
- I_k - light intensity for which extended initial slope of light curve intersects with maximum growth rate, $\text{cal cm}^{-2} \text{ day}^{-1}$
- I_s - saturation light intensity, $\text{cal cm}^{-2} \text{ day}^{-1}$
- J - heat of combustion of algae, $\text{k cal gr dry wt}^{-1}$
- k_d - decay coefficient, day^{-1}
- N_A - Avogadro's No., 6.02×10^{23} molecules mole^{-1}
- P - algal productivity, $\text{gr dry wt m}^{-2} \text{ day}^{-1}$
- P' - peak algal productivity for given depth and incident sunlight intensity, $\text{gr dry wt m}^{-2} \text{ day}^{-1}$
- Q_λ - relative quantum requirement
- T - temperature, $^{\circ}\text{C}$
- T' - temperature, $^{\circ}\text{K}$
- U - quantum of energy, mole basis, einsteins
- V - culture volume, m^3
- X - algal biomass concentration, mg l^{-1}
- X' - optimum algal biomass concentration for given depth and incident sunlight intensity, mg l^{-1}
- μ - specific growth rate, day^{-1}
- μ_N - net specific growth rate, day^{-1}
- μ_N' - optimum net specific growth rate for given depth and incident sunlight intensity, day^{-1}
- α - extinction coefficient, $\text{cm}^2 \text{ mg}^{-1}$
- θ - quantum efficiency, whole integers
- θ^{-1} - quantum requirement
- ν - frequency of light propagation, sec^{-1}
- λ - wavelength, nm
- Y_L - initial (maximum) slope of light curve, $\text{cm}^2 \text{ cal}^{-1}$

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Table 1. Summary of light saturation intensities (I_s) for different freshwater and marine microalgae reported in the literature.

Species	Temperature °C	I _s		Reference
		Illuminance ft-c	Irradiance† cal cm ⁻² min ⁻¹	
Freshwater				
<i>Chlorella pyrenoidosa</i>	25		0.036	Phillips and Myer (1954)
	25	500	0.025	Sorokin and Krauss (1962)
	26		0.057	Pickett and Myer (1966)
<i>Chlorella vulgaris</i>	25	250	0.013	Sorokin and Krauss (1962)
<i>Scenedesmus obliquus</i>	25	500	0.025	Sorokin and Krauss (1962)
<i>Chlamydomonas reinhardtii</i>	25	500	0.025	Sorokin and Krauss (1962)
<i>Chlorella pyrenoidosa</i>	25	500	0.025	Sorokin and Krauss (1962)
(7-11-05)	39	1400	0.070	Sorokin and Krauss (1962)
Marine				
Green algae (7)	20	500	0.025	Ryther (1956)
Diatoms (3)	20	1000	0.050	Ryther (1956)
Dinoflagellates (4)	20	2500	0.125	Ryther (1956)
<i>Phaeodactylum tricornutum</i>	18°		0.057	Mann and Myer (1968)

† Estimated from conversion factors in Table 5-3 from Bickford and Dunn (1972) for light source stated in reference for I_s in illuminance units.

Figure Legends

- Figure 1. Schematic diagram of large-scale outdoor algal culture with continuous flow.
- Figure 2. General relationships between algal growth rates (μ) and environmental parameters: 2(a) limiting nutrient (S); 2(b) light intensity (I); 2(c) temperature (T); 2(d) light intensity for varying temperature.
- Figure 3. Detailed general relationship between algal growth rate (μ) and light intensity (I).
- Figure 4. Thermodynamic efficiency (E) of photosynthesis as a function of wave length: 4(a) effect of wave length on $E(\lambda)$; 4(b) effect of wave length on quantum requirement (Q_λ)....*Chroococcus* (from Emerson and Lewis, 1942), ---*Navicula minima* (from Tanada, 1951), ---*Chlorella pyrenoidosa* (from Emerson and Lewis, 1943); 4(c) wave length-dependent thermodynamic efficiency [$E(\lambda)$] corrected for quantum requirement (Q_λ) from 4(b).
- Figure 5. Light utilization efficiency (E_s) according to the Bush equation, and total efficiency of photosynthesis (E_T) for $E_q = 0.2$ as a function of $I_o I_s^{-1}$.
- Figure 6. Light utilization efficiency curves: 4(a) dissipation of light with depth according to Beer-Lambert Law for incident irradiance $I_o = 0.7 \text{ cal cm}^{-2} \text{ day}^{-1}$, $I_s = 0.04 \text{ cal cm}^{-2} \text{ day}^{-1}$; 4(b) same as 4(a) but with $I_o = 0.2 \text{ cal cm}^{-2} \text{ day}^{-1}$; 4(c) light utilization efficiency (E_s) for $I_o = 0.02-0.6 \text{ cal cm}^{-2} \text{ day}^{-1}$. E_s calculated from Bush equation.
- Figure 7. Maximum expected total solar irradiance as a function of latitude and month of year. Data originally compiled by Gotaas and Oswald (1958) from U.S. Weather Bureau records.
- Figure 8. Total solar irradiance by month: 4(a) Woods Hole, Massachusetts; 4(b) Ft. Pierce, Florida. Shaded area represents range of expected values for given latitude from Gotaas and Oswald (1958).
- Figure 9. Mean daily irradiance striking surface of United States in 50 $\text{cal cm}^{-2} \text{ day}$ intervals. Modified from Thekaekara (1976).
- Figure 10. Energy spectral distribution of solar irradiance: 10(a) total spectrum; 10(b) visible spectrum. Modified from Shalef *et al.* (1968).
- Figure 11. Algal yield (P) as a function of total solar irradiance I_o using equation (29) and Ryther's model as described in text.

- Figure 12. General productivity curves: 12(a) productivity (P) as a function of algal biomass concentration (X); 12(b) productivity (P) as a function of net specific growth rate (μ_N); 12(c) biomass concentration (X) as a function of net specific growth rate (μ_N); 12(d) optimum net specific growth rate (μ_N') as a function of incident total light intensity (I_0) for varying depths (d).
- Figure 13. Effect of net specific growth rate (μ_N) on productivity (P) and algal biomass concentration (X) during mass culture experiments with marine diatoms in Woods Hole, Massachusetts: 13(a) productivity (P) curve; 13(b) biomass (X) curve. Modified from Goldman and Ryther (1975).
- Figure 14. Summary curves for productivity (P) vs net specific growth rate (μ_N) for different mass culture experiments: marine algae grown in Woods Hole, Massachusetts [curve a from Goldman and Ryther (1975), curve b from D'Elia *et al.* (1977)], marine algal grown in Ft. Pierce, Florida [curve c from Goldman *et al.* (1975)], freshwater algae grown in Richmond, California [curve d from Benemann *et al.* (1977)].

Fig. 1

Fig. 2

Fig. 3

Fig. 6

Fig. 7

Fig. 8

Fig. 9

Fig. 10

Fig. 11

ALGAL YIELD, P-gr dry wt $m^{-2} day^{-1}$

Fig. 14