INTERACTION OF EFFECTS BY ENVIRONMENTAL FACTORS ON PRIMARY PRODUCTIVITY IN PONDS AND MICROECOSYSTEMS

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Submitted to the Faculty of the Graduate School of
the Oklahoma State University
in partial fulfillment of the requirements
for the degree of
DOCTOR OF PHILOSOPHY
May, 1964

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PREFACE

In Oklahoma farm ponds primary productivity appears to be higher with a low rate of water exchange. Water exchange and other environmental factors create a wide variety of pond conditions. Laboratory microcosms provide a method by which a large number of these conditions may be studied, and provide an experimental approach to some of the complex problems of ecology.

Thanks are due many individuals whose aid was essential to successful completion of this study. Dr. Troy C. Dorris served as major advisor. Dr. Glenn W. Todd gave valuable counsel, Dr. Eddie Basler guided experiments with carbon^{14}, Dr. Clinton Miller, Dr. LeRoy Folks and Dr. Robert Morrison aided in preparation of the statistical design and Dr. J. Paul Devlin counseled with the author on computation of dissolved carbon dioxide concentration. Dr. H. T. Odum of the Institute of Marine Science, University of Texas, loaned apparatus for early portions of the study and critically read the manuscript. Mr. Neil Armstrong of the Computation Center, University of Texas, arranged for calculation of experimental results and wrote the computer program for microcosm productivity.

Mr. Sam Myers and Mr. C. S. Bassler permitted access to their ponds, Dr. Joe Gingrich of the Agronomy Department, Oklahoma State University, loaned refrigeration equipment, and Mr. Ed Allen of the Research Foundation Electronics Laboratory, Oklahoma State University, aided in

design of electronic apparatus. Mr. Kenneth Minter of the Aquatic Biology Laboratory, Oklahoma State University, and Dr. B. J. Copeland of the Institute of Marine Science, University of Texas, gave assistance and advice on many occasions. My appreciation is here expressed to these persons.

This study was supported by funds granted by the Oklahoma Oil Refiners' Waste Control Council, the National Science Foundation Research Participation Program for College Teachers and a Public Health Service Research Traineeship.

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CHAPTER I

INTRODUCTION

Rates of primary production vary considerably in farm ponds of central Oklahoma. Penetration of light in many ponds is inhibited by the presence of colloidal clay particles of a non-settling or slow-settling variety. Euphotic zones are limited to the upper few centimeters in some ponds and a euphotic zone depth greater than two meters is uncommon. Dissolved solids content of the pond waters usually is within the range of 60 to 300 mg/l (Smith, Dott, and Warkentin, 1942).

The quantity of clay particles and dissolved solids concentration in ponds is controlled by the rate of water exchange or the frequency and degree with which water is replaced as the result of inflow and outflow. Through its effect on water quality, water exchange influences primary productivity. Water exchange affects the pond environment in two ways: (1) in the concentration of dissolved minerals available for nutrition of photosynthetic organisms and (2) in reduction of light penetration by clay turbidity.

A high rate of water exchange with frequent overflow results in pond-water quality approximating that of run-off water from the watershed. Under these conditions no accumulation of dissolved minerals occurs. Many ponds with high exchange rates are continuously turbid.

A low rate of water exchange occurs when there is minimal drainage from the watershed and pond capacity is sufficient to minimize overflow;

exit is mostly by evaporation. Under such conditions build-up in ionic content may occur. Ponds with low exchange rates frequently exhibit low levels of turbidity and deep light penetration.

Two series of ponds were studied in the field with respect to photosynthetic productivity, turbidity and mineral content. Greater productivity was observed in ponds with higher content of mineral ions and lower turbidity but the separate, relative influences of the two factors could not be deduced. Laboratory experiments were performed to study the effect upon primary productivity of variations in turbidity and ionic content. A wide range of environmental conditions was simulated in the laboratory and effects upon productivity of quasi-natural populations were assessed.

Although reduction of light by turbidity was important in control of primary production rate, it was not an all-important factor in the laboratory experiments. The interaction of effects by turbidity, dissolved solids content, temperature and surface light intensity appeared to control productivity. Optimal turbidity level or light intensity was related to ionic content. Effect of turbidity on productivity was less at low temperature. Optimal ionic content was near 300 ppm.

Organisms that inhabit aquatic environments are associated in groups of plant, animal and decomposer species. Composition of the associations is regulated by a number of environmental factors. Environmental factors and organisms constitute an ecosystem (Tansley, 1935). Characteristic of ecosystems are (1) conversion and storage of energy by photosynthetic and chemosynthetic organisms, (2) transfer of energy from one organism to another, (3) dissipation of energy to the environment as heat, and (4) exchange of materials between organisms that participate in each process. All the processes are essential to continuance of organization within the ecosystem.

Since an ecosystem involves heterogeneous biological associations as well as the abiotic environment, its metabolism and maintenance is necessarily complex. Numerous processes, reactions and interactions proceed simultaneously in even the simplest communities. Interruption of any single process may alter the pattern of a whole set of processes; therefore, it is necessary to study ecosystems intact.

Systems usually must be studied without comprehension of all internal parts; that is, the investigator cannot have recourse to analysis or experimentation on individual components. The investigator proceeds without knowledge of the component parts of the system, as though the interior were hidden from view by a "Black Box" (Ashby, 1958). If the system is subjected to a series of inputs, and outputs are determined, a great deal may be learned about the concealed components. Such an approach is fruitful in studying ecosystems since most ecosystem processes are hidden from the investigator's view. Inputs used in the present study were combinations of environmental factors which are rate-controlling for metabolic processes in nature. Outputs determined were primary productivity, community respiration, standing crop of organisms, and species diversity.

Scientific treatment of a complex system does not require that all possible distinctions be made (Ashby, 1956). Microecosystems studied here have been defined in terms of measured variables. Levels of variables were selected to provide ranges indicative of natural situations within limitations of cost and convenience and sufficient for interpolation of intermediate levels (ibid).

Productivity of pond ecosystems is difficult to measure because of wide fluctuations in environmental factors that influence the systems. Control of environmental effects may be accomplished in laboratory studies of ecosystems to give inputs of definite and reproducible character. Simulation of natural ecosystems in laboratory microcosms has been used in various studies (Odum and Hoskin, 1957; Whittaker, 1961; Beyers, 1962; and McConnell, 1962). Such simulation was based on the assumption that model ecosystems are analagous to natural ecosystems, and one may be used to obtain information about the other. Natural complexity inherent in ecosystems was retained but made minimal with environmental control. Odum and Hoskin (1957) described their approach as follows: "Whereas most kinds of experiments involve isolating a part of a system for study, a microcosm experiment is designed to retain as much of the total complexity as possible, including especially the producer, consumer, regenerator, and circulating phases."

The present study is an attempt to assay effect of particular environmental factors and interaction of factors upon productivity of communities in microcosms. Reference is made to possible similarities in pond ecosystems.

CHAPTER II

LITERATURE SURVEY

Study of energy flow through producer and consumer levels of ecosystems was first formalized by Lindeman (1941, 1942) who estimated efficiency of photosynthetic producers and herbivorous and carnivorous consumers in a bog lake. He found that both efficiency of energy transfer between levels and energy loss due to respiration increased in higher levels in the food cycle of organisms. Dineen (1953) analyzed trophic stages in a pond, measured annual productivity and calculated efficiencies. McConnell (1963) related production of game fish to primary production in some Arizona impoundments. McConnell presented data that showed a strong tendency for community respiration to equal photosynthesis. Complete studies of energy tie-up, transfer and dissipation in ponds have not been made. Copeland (1963), Minter (1963) and Tubb (1963) estimated primary production, herbivore production and efficiency and described a linear succession in a series of oil refinery effluent holding ponds. Energy storage in the ponds was higher than in most aquatic habitats and significant amounts of energy were lost from the ponds by emergence of herbivores.

Much pond research has included physico-chemical measurements. Usually these have not been designed to measure variations in chemical characteristics that might be used to evaluate trophic-dynamics. Authors have alluded to variations in oxygen concentration and pH associated with organismal activity but few have quantified these variations. Phillip (1927) described pH fluctuations between 7.40 and 8.95 caused by vegetation in a lake. Schutte and Ellsworth (1955) discovered diurnal pH change as great as 3.5 pH units and pH as high as 12.6 in small African lakes. Whitney (1942) and George (1961) measured pH and oxygen fluctuations in small ponds and pointed out the dependence of these fluctuations upon photosynthesis and respiration by aquatic organisms. Megard (1962) described "diel" fluctuations in both carbon dioxide and oxygen concentration in shallow mountain lakes and estimated production from the fluctuations. Sugiura (1953) noted diurnal variations of oxygen content in fresh and marine waters and computed oxygen consumption and production in a moat based on diurnal variation in oxygen content. Wiebe (1931) found extremes of oxygen concentration of 89 to 268% saturation in a single day in a pond with a bloom of blue-green and green algae. Laurie (1952) recorded differences in oxygen concentration associated with masses of vegetation in a pond. He found characteristic afternoon maxima and early morning minima in all areas within the pond, but with more pronounced changes in beds of vegetation. A stream tributary to the pond had little vegetation and a diurnal oxygen cycle inverse to that in the pond.

Rates of primary or photosynthetic production have been determined for a wide variety of aquatic habitats based on change in oxygen or carbon dioxide content of water. Odum (1956), Ryther (1956), Verduin (1956), Lund and Talling (1957), and Pomeroy (1961) described methods used in estimation of primary productivity in fresh waters. Strickland (1960) reviewed methods used in marine waters. Talling (1961) reviewed environmental measurements of photosynthesis including aquatic environments.

Few estimates of primary productivity in ponds have been reported to date. Odum and Hoskin (1958) reported the primary productivity of Stewart Farm Pond in North Carolina. Hepher (1962) measured primary productivity in Israelian fish ponds with reference to fertilization experiments. Copeland, Butler and Shelton (1962) studied photosynthetic productivity of a small pond subjected to frequent influxes of organic matter. Copeland and Whitworth (1963) measured photosynthetic oxygen production in several fertile ponds in central Oklahoma.

Most productivity research in ponds has been related to fish management. Edmister (1947), Bennett (1962) and Coker (1954) have dealt with principles of fish-pond productivity. Neess (1949) reviewed the pond-fish industry of Europe and successful European fertilization of ponds to increase yield. Wallen (1955) discussed limnological characteristics of ponds which might be related to high fish production. Moorman (1957) related some biological and physical factors to success of fish in Iowa farm ponds.

Unique physical and biological characteristics of muddy ponds have been considered infrequently. Burris (1954) studied the developing bottom fauna of a newly-constructed turbid pond. Hambric (1953) compared the bottom fauna in clear and turbid ponds. Claffey (1955) found plankton productivity to be reduced with increase in turbidity caused by silt particles. Irwin (1945) and Irwin and Stevenson (1951) studied the nature of turbidity-causing particles with reference to clarification. Keeton (1959) determined the value of oil field brine for clarification of turbid ponds and described some of the limnological conditions that result from such treatment. Wallen (1951) and Butler (1963) have dealt with temperature characteristics in turbid ponds.

Biota of ponds have been studied by many authors. Burris (1954) and Hambric (1953) studied bottom fauna in farm ponds. Wallen (1949) studied the plankton community in a small pond and Wiebe (1930) investigated plankton populations in fish ponds. Ward (1940) studied seasonal patterns of entomostraca in ponds. Minter (1952) studied distribution of entomostracans in a Kansas pond. Organismal constituents of the communities in a New Zealand pond were described by Byars (1960) and in a Minnesota pond by Dineen (1953).

Farm ponds in Oklahoma are important economically for soil conservation and erosion control and for water storage for livestock and other farm use (Carlander, Campbell and Irwin, 1963). The number of ponds in Oklahoma has been estimated at over 300,000 (Anon, 1960) and over 100,000 by Wallen (1955) who has listed other, less common, uses for pond waters. Use of farm ponds as a water supply has prompted studies which include limnological measurements. Willrich (1961) reviewed the properties of pond water and treatment required prior to domestic use. Pond age apparently affected color, turbidity and nitrate concentration, and a relationship existed between hardness of pond water and turbidity. Willrich (ibid) and Esmey, et al. (1955) discussed the influence of watershed characteristics on pond water quality. Calkins (1947) described the structure of various types of farm ponds including the types of ponds considered in the present study.

CHAPTER III

METHODS

Field Studies

Net production and night respiration in pond ecosystems were estimated from diurnal changes in concentration of dissolved oxygen (Odum, 1956; Odum and Hoskin, 1958). Oxygen content of water samples was measured by the Alsterburg (Azide) modification of the Winkler method (APHA, 1960) at two- or three-hour intervals over a 24-hour period. The rate of change of dissolved oxygen with respect to time, $\frac{\partial O_2}{\partial t}$, when plotted against time, yielded a curve representing a series of first order differential equations. Integration by planimetry yielded (1) net primary productivity as the integral of the positive portion of the graph and (2) night respiration as the integral of the negative portion of the graph. Total respiration was taken to be the hourly mean of $\frac{\partial O_2}{\partial t}$ at night x 24 hours. Gross primary productivity was obtained by adding 12 x hourly mean of $\frac{\partial O_2}{\partial t}$ at night to net productivity. Corrections for diffusion were made by the method of Odum and Hoskin (1958).

Estimates of dissolved solids concentration were made by weighing the residue of a sample after ignition and by measurements of electrical conductivity (APHA, 1960). Turbidity was measured with a Bausch and Lomb "Spectronic 20" Colorimeter calibrated against a Jackson Turbidimeter. Depth of euphotic zones was measured with a Gem submarine photometer. Solar radiation was measured continuously with a pyrheliometer at the Oklahoma State University weather station.

Laboratory Studies

Metabolism of microecosystems was studied under controlled conditions. Black polyethylene sheeting was used to exclude extraneous light from an area 10 x 12 ft within a controlled-temperature laboratory. A framework was constructed to hold 32 microcosms. Batteries of fluorescent lights were suspended at variable distances above the microcosms (Fig. 1). Rectangular polyethylene containers of 10-liter capacity were used as receptacles for the microecosystems. Surface area of water was 460 cm^2.

Light intensity, temperature, dissolved solids content and turbidity were independently variable environmental factors in laboratory studies. Combinations of two light intensities, two temperatures, four dissolved solids concentrations, and four turbidities formed 64 individual experiments.

Gro-Lux fluorescent lamps (Sylvania Electric Products Co.) were used as a light source. Gro-Lux tubes (Fig. 2) are most productive in those wave-lengths of light that are important for photosynthesis (Dunn and Bernier, 1961). Peaks in the emission spectrum occur at about 450 and 670 mμ. Light absorption by algae is primarily in the blue and red ends of the spectrum, 400 to 480 mμ and 650 to 680 mμ. Similarity between quality of light produced by Gro-Lux tubes and light required for photosynthesis is shown in Fig. 2. Absorption spectra of whole <u>Chlorella</u> cells and isolated pigments are after Emerson and Lewis (1943). Radiation of sunlight ranges from about 300 mμ to 1600 mμ with a broad maximum between 450 and 650 mμ (Hutchinson, 1957). Standard cool white and daylight fluorescent lamps are rich in medium-length radiation (430 to 590 mμ) and poor in the red end of the spectrum (Dunn and Bernier, 1961).

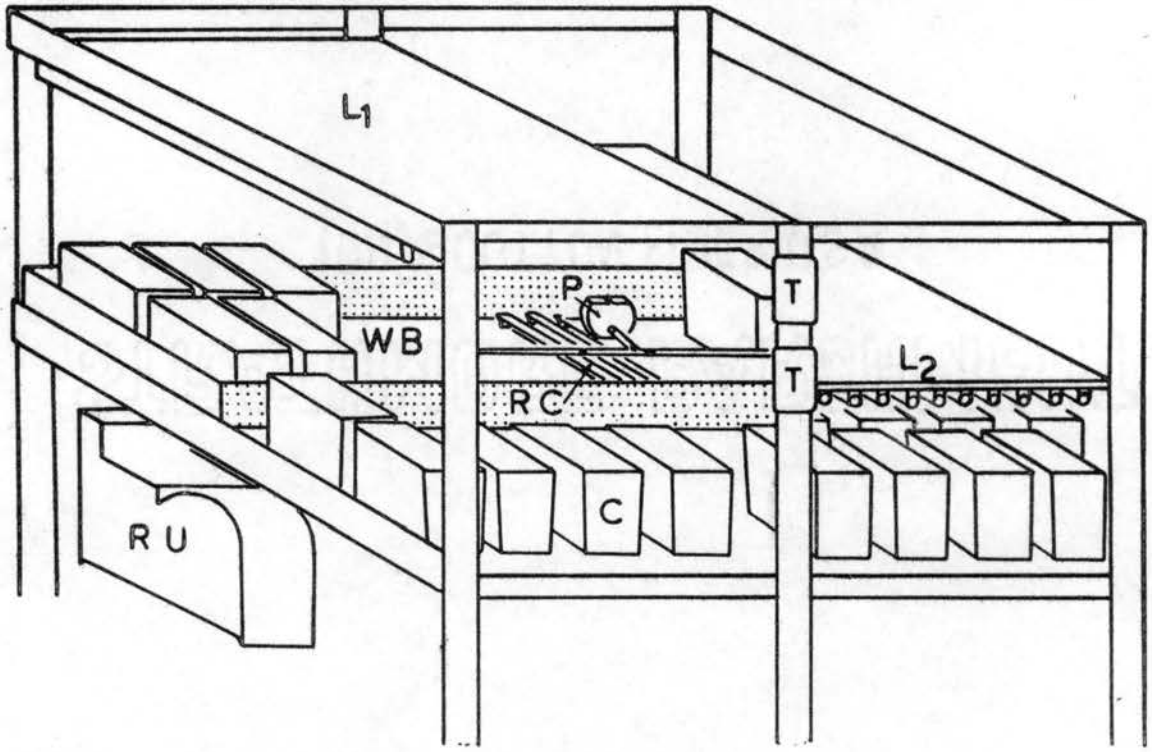


Fig. 1. Physical set-up for microcosm studies. L_1 = light bank for low light intensity, L_2 = light bank for high light intensity, RU = refrigeration unit, RC = refrigeration coils, WB = cold temperature water bath, P = circulation pump, T = timer switch for lights, C = microcosm container.

Light intensities of 400 and 800 foot candles at water surface were used in experiments. Gro-Lux lamps produced about one-third less light than cool white lamps; cool white lamps at identical distances above the water surface produced 600 and 1200 foot candles. Measurements of light intensity were made with a Weston photometer. Lamps were controlled by two timer switches, half of the lamps in each bank were controlled by

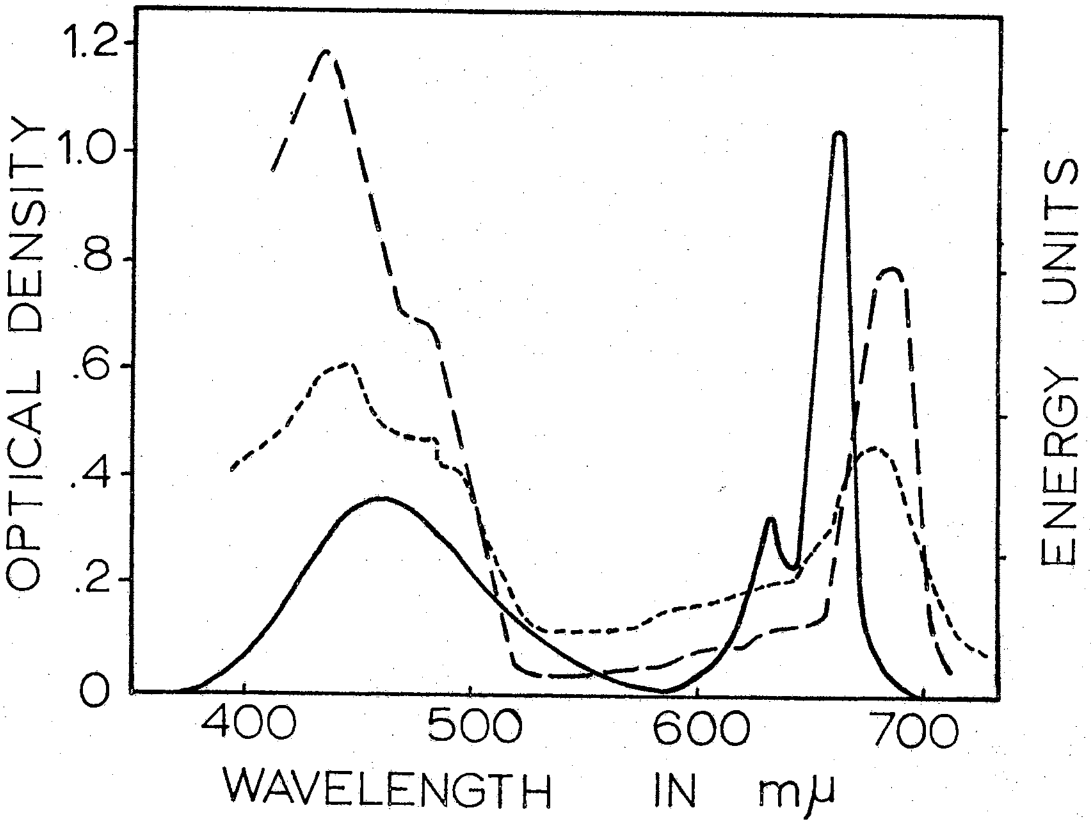


Fig. 2. Light emission spectrum for Gro-Lux fluorescent lamps and absorption spectra for algae and algal pigments. Solid line = Gro-Lux lamps, dashed line = whole *Chlorella* cells, dotted line = extracted pigments of *Chlorella*. Energy units are arbitrary.

one switch and half by the other. The switches were set 15 minutes apart, providing step-wise increase and decrease in illumination when lights were turned on or off. Illumination was for 12 hours daily.

Experimental temperatures were established at approximately 11 and 23 C. Metabolism of 32 microecosystems was studied at each temperature. The lower temperature was established by placing microcosm containers in a bath held at 11 C with a refrigeration system and the higher was at the ambient temperature of the laboratory. Water temperature fluctuated less than 3 C over a 24-hour period. Typical characteristics of the controlled environment during a sampling period are shown in Fig. 3.

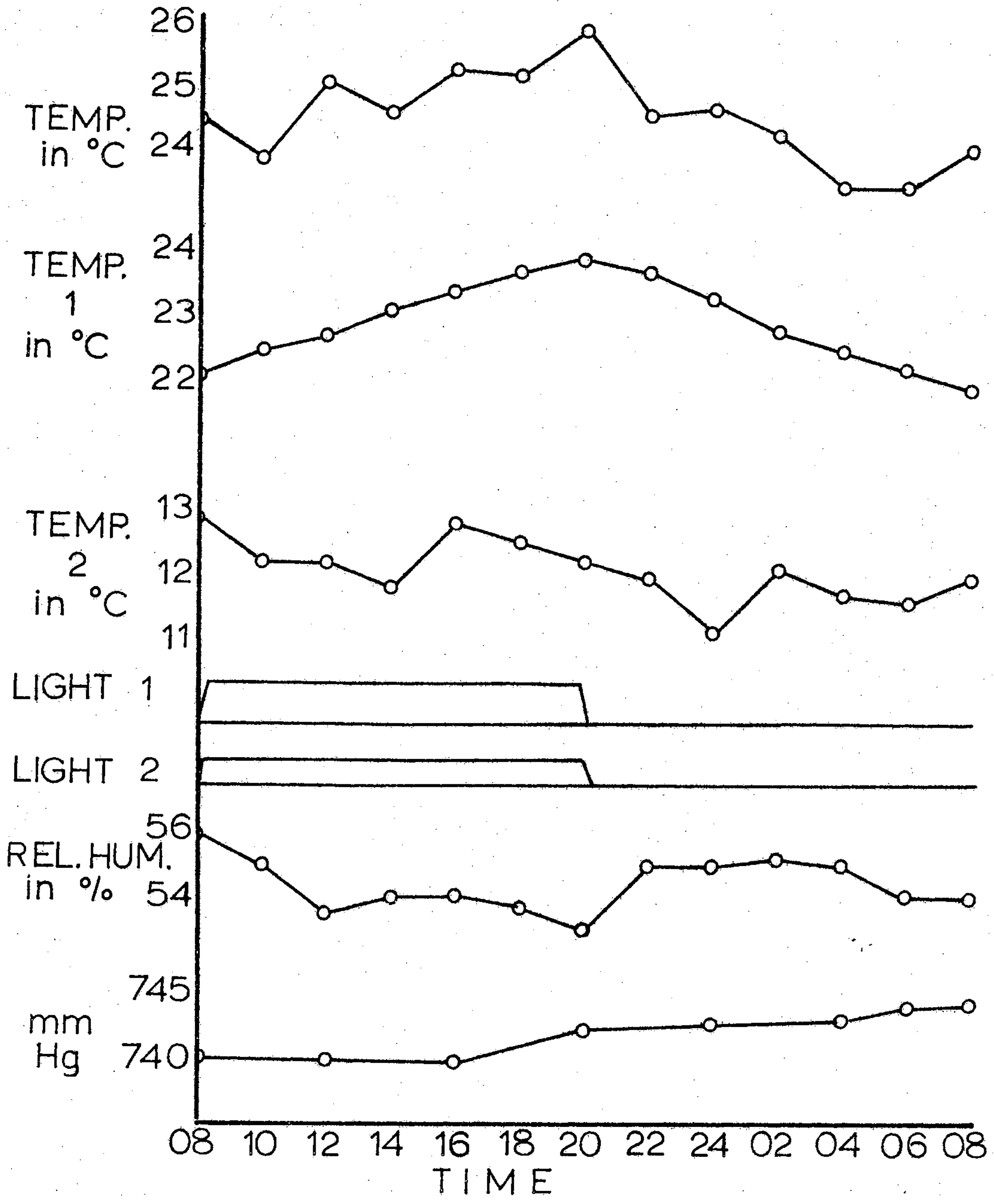


Fig. 3. Typical characteristics of environmental factors in microcosm experiments. Temp. = air temperature in controlled environment laboratory, Temp. 1 = higher temperature in microcosms, Temp. 2 = lower temperature in microcosms.

Since clay particles which form the major source of turbidity in ponds coalesced and settled out even with frequent stirring, a brown dye was used to create light penetration levels equivalent to turbidity of

0, 25, 50, and 75 parts per million of non-organismal turbidity. Turbidity from the dye remained stable throughout the experimental period.

Four levels of ionic concentration (total dissolved inorganic solids) were prepared with pond water and deionized water, to which were added a mixture of:

$Ca(NO_3)_2 \cdot 4H_2O$

NH_4NO_3

KH_2PO_4

$MgSO_4 \cdot 7H_2O$

to adjust concentrations to 75, 150, 300, and 600 mg/liter (parts per million). Analysis of the pond water and the known quantities of chemicals added are shown in Table I. Methods used to estimate total dissolved inorganic solids and turbidity were the same as in field studies.

During sampling periods, microcosms were stirred at 2-hour intervals to prevent microstratification of dissolved gases. A motor driven stirrer was used in such a manner as to cause minimal disturbance at the water surface.

Microcosm Metabolism

Net productivity and night respiration were estimated from analysis of changes in concentration of carbon dioxide in a manner similar to that used for oxygen concentration. Photosynthesis results in use of carbon dioxide and its removal from the water. Rate of change of carbon dioxide concentration with respect to time, $\frac{\partial CO_2}{\partial t}$, was plotted against time for 24-hour periods (Fig. 4). Net production was obtained by planimetric integration of the negative portion of the curve formed by the plot. In similar fashion night respiration was taken as the integral of the positive portion of the rate-of-change curve. Total respiration was obtained by taking 2 x night respiration. Gross primary productivity was determined by adding night respiration to net primary productivity.

TABLE I

IONIC CONCENTRATION OF MICROCOSM WATER IN MG/L

Ion	Dilution 600 ppm	 300 ppm	 150 ppm	 75 ppm
Na and K	36	18	9	5
Ca	94	47	24	12
Mg	39	20	10	5
NH_4	1	.5	.2	.1
Fe	.04	Tr.	Tr.	Tr.
SO_4	96	48	24	12
Cl	41	20	10	5
Fl	7	4	2	1
PO_4	35	18	9	5
NO_3	88	44	22	11
HCO_3	162	81	40	20

Carbon dioxide concentrations may be calculated from pH data and alkalinity (de Martini, 1938; Moore, 1939; Dye, 1944; Park, Hood, and Odum, 1958) or from pH data and carbonic acid titration curves (Beyers and Odum, 1959 and 1960; Beyers, 1962a). During 24-hour sampling

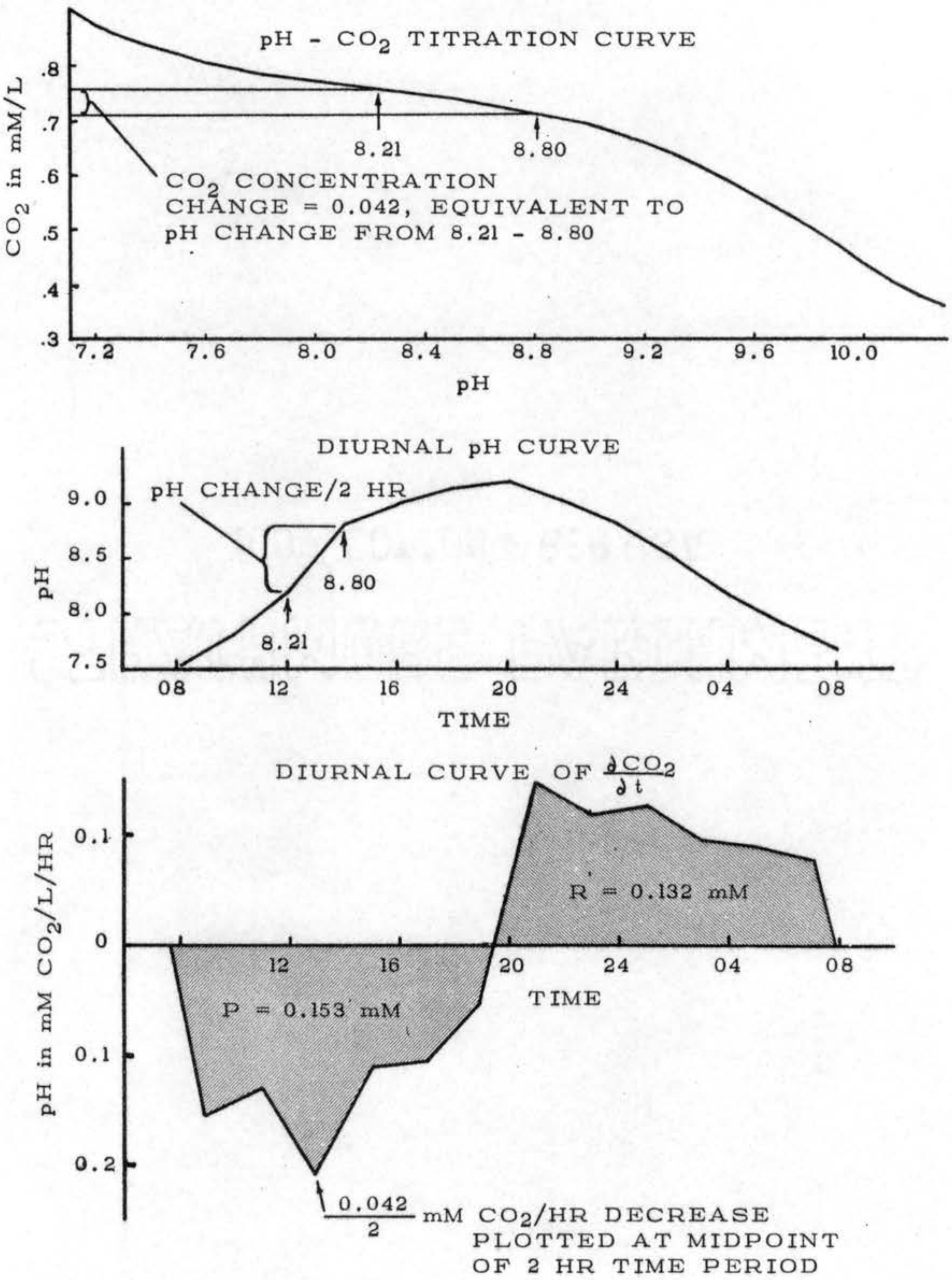


Fig. 4. Representative pH - CO_2 titration curve and curves of diurnal variation in pH and $\frac{\partial CO_2}{\partial t}$. Change in CO_2 concentration for pH change in a 2-hour interval is determined from the titration curve and $\frac{\partial CO_2}{\partial t}$ is plotted against time. Net photosynthetic productivity (p) and night respiration (R) are obtained by planimetry.

periods, pH in each microcosm was determined at two-hour intervals with a Beckman Zeromatic pH meter. Continuous recordings were made for some microcosms with the pH meter and a Rustrak amplifier and recorder. Alkalinity was determined by titration (APHA, 1960).

The equations of de Martini (1938) and Moore (1939) are based upon the dissociation constants for carbonic acid. These dissociation constants, defined in equations 1 and 2, vary with the water in question, and constants taken from the literature may differ from the unknown constants of experimental waters.

$$K_1 = \frac{[H^+]\ [HCO_3^-]}{[H_2CO_3]} \qquad K_2 = \frac{[H^+]\ [CO_3^=]}{[HCO_3^-]} \qquad (1,\ 2)$$

Equation 3 was formed by combination of the separate equations of de Martini and Moore and was more convenient for the type of calculations made in this study.

$$\text{Total } CO_2 = \frac{\text{Alk}}{1 + 2\,\frac{K_2}{(H^+)}} \left[1 + \frac{K_1}{(H^+)} + \frac{(H^+)}{K_1} \right] \qquad (3)$$

Titrations with carbonic acid were based upon the premise that the pH of microcosm water is a function of carbon dioxide dissolved in the water (Beyers, 1962a). A curve of pH changes can be translated into changes in carbon dioxide concentration. The method of titration of Beyers and Odum (1959, 1960) was used to titrate through the pH range found in microcosms. Deionized water was saturated with carbon dioxide in a specially constructed burette (Beyers, 1962a) and added in increments of 0.1 to 0.4 ml to a 300 ml sample of microcosm water. After each addition the sample was stirred gently with a magnetic stirrer and the pH determined. Carbon dioxide present in each increment of titrant was determined using Beyer's (ibid) tables of carbon dioxide concentration and curves were constructed from pH changes associated with each carbonic acid addition. A representative titration curve and its use in determining diurnal carbon dioxide change in a microcosm is shown in Fig. 4.

Productivity and respiration in microecosystems were estimated from diurnal changes in dissolved oxygen content as in field studies but with 30 ml samples.

Radioactive carbon^{14} in the form of $Na_2C^{14}O_3$ was used to estimate the non-photosynthetic or dark contribution to total carbon dioxide uptake. Samples of ecosystem components (2.0 ml) from microcosms were exposed to $Na_2C^{14}O_3$ in Warburg vessels with dual sidearms. 0.25 ml labeled Na_2CO_3 was placed in one sidearm and 1.0 ml 1 N HCl in the other. Vessels were darkened by wrapping with aluminum foil. The Na_2CO_3 was introduced into the reaction vessel and the vessels were placed in a Warburg water bath held at either 11 or 23 C. Carbon^{14} uptake was allowed to procede for one hour and the reaction was then stopped by introduction of the HCl. Duplicate samples were treated simultaneously but were exposed to light. Each sample was plated out in a planchet, dried, and counted with a Picker Proportional Gas Flow Counter. An additional sample from each ecosystem was treated to obtain the ash-free dry weight. Counts were corrected for self-absorption from a graph previously constructed.

Ash-free dry weight was estimated at each sampling period by removing a 50 ml sample of thoroughly mixed water from each microcosm, evaporating in tared crucibles, igniting, and weighing.

Estimates of chlorophyll concentration were made at the final sampling period. Algae were removed from 100 ml samples of microcosm water by Millipore filtration and pigments extracted in 90% acetone at 5 C for 24 hours. Optical density of chlorophyll extracts was measured with a Beckman DU Spectrophotometer (Richards and Thompson, 1952) or a Bausch and Lomb "Spectronic 20" colorimeter (Copeland, 1963). Optical densities at 665, 645, and 630 mμ were read with the spectrophotometer and concentrations of chlorophylls a, b, and c computed with the equations of Richards and Thompson (1952). Optical density at 665 mμ as measured with a "Spectronic 20" may be converted to chlorophyll a concentration using a calibration curve (Odum, McConnell, and Abbott, 1958). Fig. 5 is a calibration curve, colorimeter readings versus concentration determined spectrophotometrically, taken from microcosm samples. Results were expressed in mg/L chlorophyll a in the acetone extracts. Conversion to mg chlorophyll a/liter of water sampled is by multiplication by $\frac{\text{ml acetone}}{1000 \text{ x liters water}}$. Some extracts also were read at 510 and 480 mμ on the spectrophotometer and carotenoid pigments computed.

Microecosystems were seeded with organisms in the original pond water plus an inoculum from six ponds of varying type. Counts of organisms present in the microcosms were made with a Palmer counting cell and population diversity graphs were constructed (Fig. 8) using the procedure of Yount (1956).

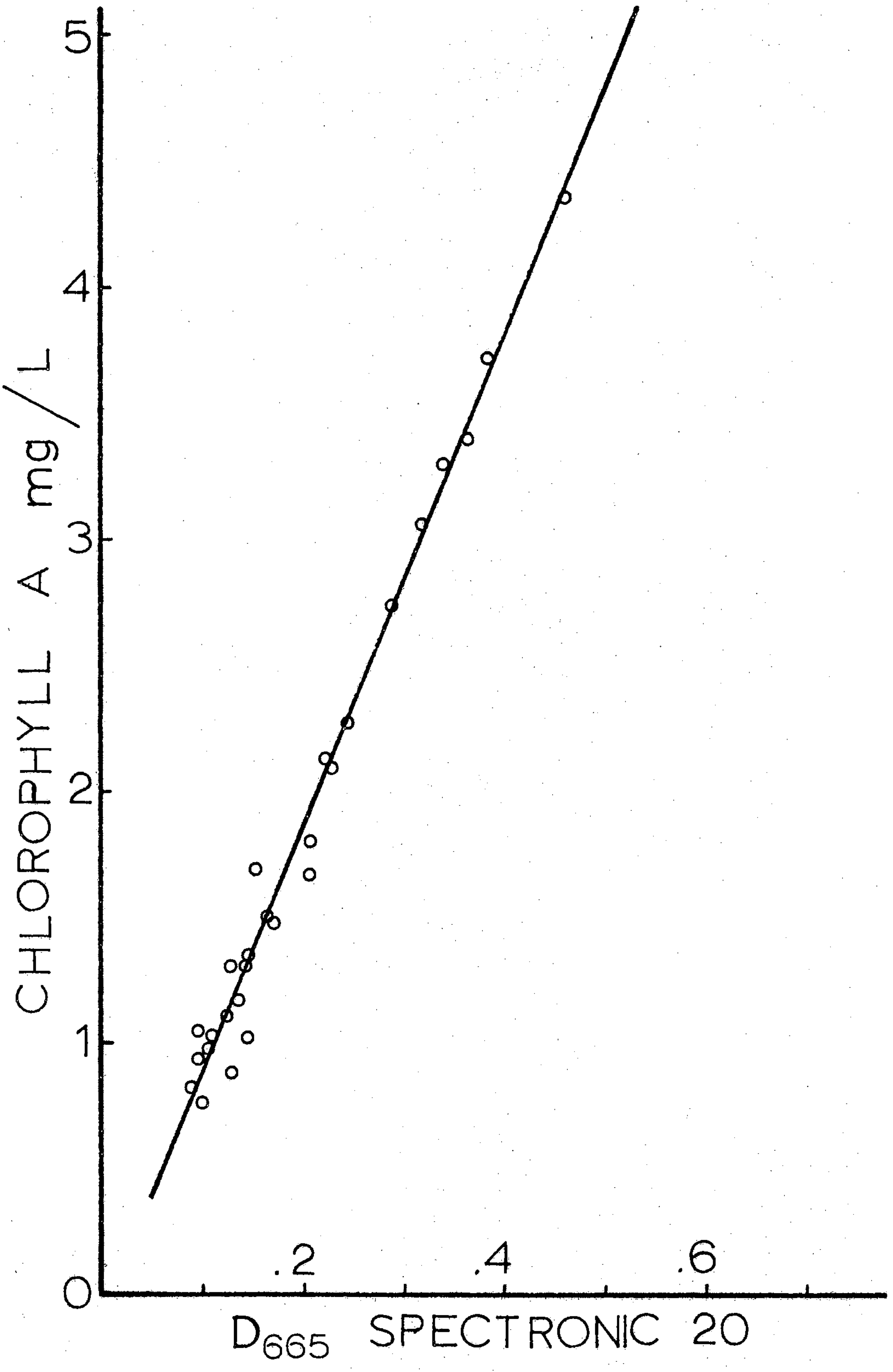


Fig. 5. Calibration curve for conversion of optical density measured colorimetrically to concentration of chlorophyll in the extract.

CHAPTER IV

TURBIDITY IN OKLAHOMA FARM PONDS

Most farm ponds in central Oklahoma are subject to fluctuating water levels and extremes of inflow and outflow. Characteristic muddy appearance of many ponds results from clay particles in suspension in the water. Much of the exposed land surface of central Oklahoma is Permian red clay (Hall, 1949) from which the particles are washed by runoff.

The clay particles responsible for pond turbidity approach colloidal dimensions (between 0.5 and 5 μ in diameter) and settle out of suspension slowly. Particles are a montmorillonite clay (Irwin and Stevenson, 1951), usually flattened and disc-like in shape.

Wind action and convection currents tend to keep particles in motion and suspended in the water medium. Brownian movement aids in keeping the particles in continuous motion. Aggregations of particles build up when they come in contact and adhere to one another. Large aggregates precipitate more rapidly than do individual particles.

Tendency to flocculate and precipitate is affected by an electrical potential borne by the particles. If electrical potential is small, there is little repulsion between particles which may coalesce upon collision. Resultant larger particles have sufficient mass to settle out under the influence of gravity. If electrical potential is large, particles repel one another when they approach, preventing flocculation and settling.

Electrical potential results from a double layer of charges on the particles. An inner negative layer is present around the surface of an alumino-silicate core. An outer positive layer is formed by cations that surround the core. Cations in the outer layer are exchanged with cations in the surrounding medium. Potential on a particle varies directly with the rate of exchange of cations.

Attraction which binds cations to the core is dependent upon the distance between core surface and cation. Large ions (or ions effectively large because of hydration) cannot be held as close to the core surface as small ions and, therefore, are exchanged more easily with other ions in the water.

Association of cations with clay particles affects ionic content of pond water and level of clay turbidity. Consequently, other limnological factors are related. In general, as conductivity and hardness of water increase, turbidity decreases (Esmey, et al., 1955; Willrich, 1961). Calcium and magnesium, which are principal contributors to hardness and specific conductance of water, are active in flocculation of suspended matter (Hodges and Shanklin, 1958).

Irwin has suggested increasing hydrogen ion concentration as an aid in precipitating clay suspensions in ponds (Irwin, 1945; Irwin and Stevenson, 1951). Hydrogen ions are the smallest and are attracted most strongly to the clay core. Electrical potential of particles is at a minimum when the cation layer is composed of hydrogen ions. Mutual repulsion by particles is minimal, floculation is relatively rapid, and turbidity may be cleared. Precipitation is also stimulated by increase of other cations in a pond as by addition of gypsum (Esmey, et al., 1955) or oil field brine (Keeton, 1959).

A natural system for clearing clay turbidity in ponds exists in the activity of producer and decomposer organisms. Organismal changes in carbon dioxide concentration affect hydrogen ion concentrations in pond water. Carbon dioxide dissolved in water forms carbonic acid which is dissociated into hydrogen and bicarbonate ions. Number of hydrogen ions in water with dissolved carbon dioxide is greatly increased over that in pure water. Daily fluctuations in hydrogen ion concentration as a result of productivity and respiration initiate flocculation and clearing. When pond water is static a noticeable amount of clearing may occur. When turbidity-causing particles are added frequently to a pond with runoff water, effect of natural clearing is minor in comparison to the turbidity load. Microscopic examination has shown that particles adhere to algal and bacterial cells, further removing turbidity-causing particles as moribund organisms settle to the bottom.

The nature and extent of a pond's watershed affect the limnological characteristics of the pond water. Reports in the literature are not in agreement as to the type of watershed which yields greatest or least turbidity. Esmey, et al., (1955) found that small, well-grassed watersheds used only for collection of water produced more turbid water than either cultivated or pastured watersheds. Willrich (1961) quoted Daniels' report that ponds that cleared up after rain had considerable cultivated land in their watershed while some ponds that stayed muddy had grassed watersheds. Irwin (1954) found highly turbid pond waters drained from cultivated fields or non-grassed areas such as county roads.

Productive bodies of water are located in fertile watersheds. Mineral content of pond water varies with that of the surrounding land

and increases in a pond as evaporation occurs. Dilution of pond water by runoff water decreases mineral content of the water (Willrich, 1961). Greater stability of chemical and physical characteristics occurred in pond waters from grassed watersheds. Greater variability was associated with cultivated watersheds. Hardness fluctuated more and was significantly higher in ponds with cultivated watersheds than in those with completely grassed watersheds (ibid).

Of fundamental importance in control of pond water quality is the rate of water exchange. Water exchange rate determines whether or not enrichment by evaporation can occur. Further, the amount of clay turbidity washed into a pond is controlled by water exchange rate. Willrich (ibid) pointed out the need for research in this area in order that pond waters might be improved as a source for domestic water. He found that size of watershed did not affect turbidity and color but that ratio of watershed area to pond storage capacity did. This ratio with frequency, rate, and amount of precipitation on the watershed, and nature of the soil and cover on the watershed, determine rate of water exchange. Since pond water is affected by many factors which are difficult to quantify, water exchange rate, which reflects these factors and which can be measured at the pond itself, is of genuine significance.

CHAPTER V

PRODUCTIVITY IN FARM PONDS

Primary productivity by communities in two sets of farm ponds was studied during the summer, 1960, 61 and 62. Myers Ponds have a unique construction (Fig. 6). The upstream pond receives water from a drainage area of approximately 180 acres of grassland. It fills and overflows relatively frequently and, therefore, has a maximal rate of water exchange. The downstream pond is directly below the upstream pond and essentially has no drainage area. Overflow from the upper pond is shunted around the lower pond by a canal. The lower pond gains water by precipitation directly upon the pond surface or from the upstream pond through a pipe. It loses water only by evaporation and seepage and has minimal water exchange.

Bassler Ponds are three ponds in series in a common drainage (Fig. 7). Upper ponds reduce the watershed for lower ponds by retaining some water which otherwise would enter lower ponds. Water exchange rates are progressively lower in more downstream ponds.

Water in Myers Lower Pond was clear at all times. Turbidity fluctuated from about 6 to 15 ppm, primarily as a result of changes in plankton populations. Dissolved solids content was usually 120 to 180 ppm but changed with dilution by precipitation and drawdown of the upper pond. Concentration occurred by evaporation. Both turbidity and ionic content fluctuated more widely in the upper pond than in the lower.

Turbidity was intermediate to other ponds in the area and fluctuated from 50 to 70 ppm after rains, to 20 to 30 ppm after flocculation and settling had occurred. Extremely low turbidity in the upper pond and high mineral content in both ponds in 1962 followed a long period of low precipitation. Evaporation during the winter and spring of 1962 greatly reduced water volume in the ponds.

The upper two ponds in the Bassler series were continuously muddy although measured turbidities fluctuated widely. Turbidity in upstream Pond A was 200 to 400 ppm, in middle Pond B 100 to 200 ppm and in downstream Pond C 20 to 40 ppm. Turbidity gradient from ponds A to C was about 10:1. Dissolved solids concentration was higher than in Myers

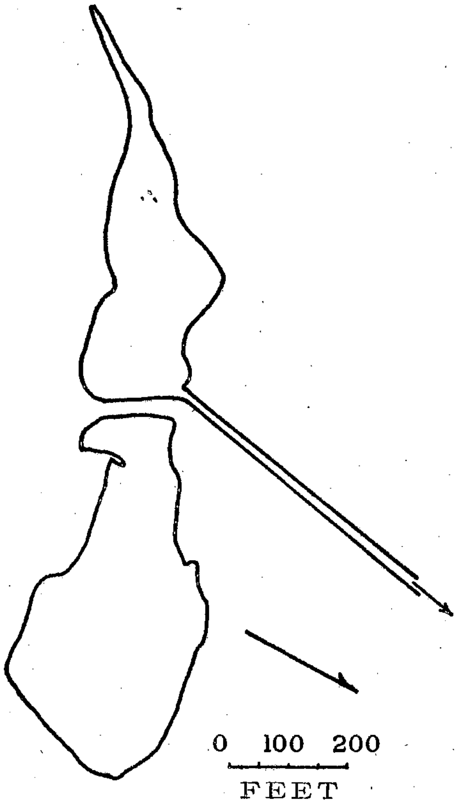


Fig. 6. Map of Myers Ponds.

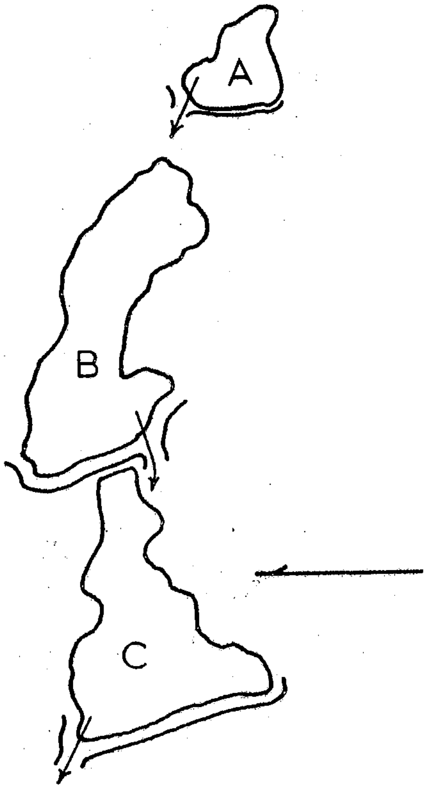


Fig. 7. Map of Bassler Ponds.

Ponds. Dissolved solids content in Pond A was less than that of Ponds B and C which were similar in concentration.

Measured Productivity

Productivity in Myers Lower Pond is among the higher values reported for small bodies of water (see Tables II and III for comparison). Copeland and Whitworth (1963) measured productivity in small, fertile ponds in which values ranged from 4 to 26 g $O_2/m^2/day$. Only one of the ponds studied by them displayed a high level of inorganic turbidity, and productivity in that pond was lowest among the ponds studied. Bassler downstream Pond C was as productive (3.6-9.3 g $O_2/m^2/day$) as the least productive pond of Copeland and Whitworth (4.4-5.7 g $O_2/m^2/day$). Stewart Farm Pond in North Carolina produced 2.2 to 4.5 g $O_2/m^2/day$ (Odum and Hoskin, 1958). Ponds with continuous organic enrichment have a high rate of photosynthetic production. Spring and summer production frequently exceeded 20 g $O_2/m^2/day$ in oil refinery effluent holding ponds (Copeland, 1963) and sewage stabilization ponds (Bartsch and Allum, 1957).

Ratio of Productivity to Respiration

Ratio of productivity to respiration (P/R ratio) has been used to classify communities (Odum, 1956). Steady-state metabolism in a community results in a P/R ratio of one unless an outside source supplies organic matter to the community. In the steady state, carbon dioxide used in photosynthesis is balanced by respiratory release of the gas and oxygen demand for respiration is balanced by oxygen production during photosynthesis. P/R ratio in any closed ecosystem must approximate

TABLE II

COMMUNITY METABOLISM IN FARM PONDS,

SUMMER 1960, 61, 62*

Year	Pond	Gross Productivity g O_2/M^2/day	Community Respiration g O_2/M^2/day	P/R Ratio	Turbidity ppm	Conductivity μmho/cm^2
1960	Myers Upper	4.9	5.6	0.7	25	244
	Lower	16.1	9.9	1.3	8	284
1961	Upper	2.4	5.5	0.4	44	165
	Lower	13.6	5.8	2.3	12	275
1962	Upper	2.4	3.4	0.7	16	220
	Lower	5.1	5.0	1.0	12	380
1960	Bassler A	0.4	0.6	0.7	250	325
	B	3.3	3.1	1.1	103	403
	C	3.6	4.1	0.9	25	400
1962	A	0.3	0.4	0.7	400	
	B	2.1	1.8	1.2	275	
	C	9.3	8.3	1.1	29	

* Mean values for seven sampling dates, Myers Ponds, 1960; two sampling dates, Myers Ponds 1961; one sampling date, Myers Ponds, 1962; two sampling dates, Bassler Ponds, 1960 and 62.

TABLE III

PRODUCTIVITY IN SOME PONDS AND OTHER SMALL AQUATIC HABITATS, ESTIMATED FROM DIURNAL CHANGES IN OXYGEN CONCENTRATION OR LIGHT AND DARK BOTTLES

Author	Year	Habitat	Productivity g $O_2/m^2/day$
Copeland, Butler and Shelton	1962	Pond	1.1 - 7.3
Copeland and Whitworth	1963	Farm Ponds	4.4 - 27.4
Talling	1955	Lagoon	4.0
Ratzlaff	1952	Roadside Ditches	2.7 - 5.1
Megard	1962	Small Mtn. Lakes	2.0 - 4.1
Hepher	1962	Fish Ponds	4.4 - 22.6
Wiebe*	1931	Fish Ponds	0.7 - 6.5
Sugiura	1953	Moat	8.5
Odum and Hoskin	1958	Farm Pond	2.2 - 4.5
Sitaramiah	1961	Pond	5.7 - 8.6
Odum and Wilson	1960	Pond Pond	1.5 - 12.0 5.3 - 14.7

* Estimated from oxygen concentrations reported by the author listed.

unity over a long period of time. In open systems such as most ponds, allochthonous material adds to the oxygen demand and its oxidation results in addition of carbon dioxide to the system. Respiration may then exceed production with a resultant P/R ratio less than one. With frequent addition of allochthonous organic matter a pond continuously may display a P/R ratio less than one (Copeland, et al., 1962). A P/R ratio greater than one occurs when productivity exceeds respiration. Such a ratio is accompanied by storage of organic matter.

The P/R ratio in Myers Lower Pond usually exceeded one while the ratio in the upper pond was characteristically less than one. In the lower pond P/R ratios were greater than one except on two sampling dates when heavy cloud cover occurred. High P/R ratios in the lower pond were balanced by temporary storage and subsequent respiration during adverse weather conditions of low light and temperature, particularly during late fall and winter, resulting in an annual P/R ratio of approximately one. In the upper pond a P/R ratio less than one resulted from high respiratory oxygen requirement by organic matter washed into the pond from the watershed.

Photosynthetic oxygen and diffusion of oxygen from the atmosphere must satisfy respiratory oxygen demands of pond communities or the ponds may become anaerobic. Low level productivity accounted for only 40 to 70 % of dissolved oxygen in the more turbid ponds on most sampling dates. Community respiration exceeded productivity, sometimes by several times, in turbid ponds but diffusion contributed sufficient oxygen to prevent anaerobiosis. Complete depletion of oxygen did not occur at the bottom of the tropholytic zone in either Myers pond under optimal summer conditions.

Efficiency

Efficiency of producers in converting solar energy to chemical energy in the form of organic compounds may be computed from gross photosynthesis and radiation data. Total solar radiation in cal/cm^2/hr was recorded by the Oklahoma State University weather station and 50% of total radiation was considered to be photosynthetically active (Edmondson, 1955; Ryther, 1956). Efficiency was calculated on the assumption that 112,000 calories is required to form (CH_2O) equivalent to one mole oxygen (Krauss, 1956) as in the photosynthetic equation:

$$CO_2 + 2\ H_2O \longrightarrow (CH_2O) + H_2O + O_2. \qquad (4)$$

Approximately 3740 calories are required to form (CH_2O) equivalent to one gram oxygen produced. Because producer organisms form other products with less energy content than carbohydrates, Copeland (1963) used 3500 cal/g O_2, the same figure used in this study, and Beyers (1962a) used 3000 cal/g CO_2 in calculation of efficiency. Efficiency in Myers Lower Pond varied from 0.6 to 2.0%. Most values were between 1.0 and 1.8% and the mean efficiency was 1.3%. Efficiency in Myers Upper Pond varied from 0.2 to 0.6% and the mean value was 0.4%. Efficiency in Bassler Pond C was about 1%, in Pond B about 0.2% and in Pond A about 0.03%. Efficiency in these ponds was directly related to productivity. Maximum efficiency of 2.0% occurred in the pond with greatest productivity. Environmental factors such as turbidity which were limiting to productivity also appeared to reduce photosynthetic efficiency. Copeland (1963) reported efficiencies that were maximal with high productivity and minimal with low productivity. Greatest efficiency recorded by Copeland in organically enriched effluent holding-ponds was 3.9% under optimal spring conditions.

CHAPTER VI

PRODUCTIVITY IN MICROCOSMS

The rate at which energy is converted and stored and at which carbon is fixed by chlorophyll-bearing plants under the influence of light is primary or photosynthetic productivity. A small percentage of light energy received by photo-autotrophic organisms is transformed and stored in the form of reduced organic compounds. Some of the transformed energy is used by the producer to drive life processes. Other organisms derive energy from the initial storage by using producer biomass as an energy source. The two types of oxidative release of energy are primary contributors to community respiration. Primary production rate is influenced by environment of the photosynthetic organisms. Temperature, light intensity, carbon dioxide concentration and dissolved solids concentration are important environmental variables. Production rates also are influenced by biotic elements of the ecosystem, viz. the kinds and numbers of producer organisms, as well as organisms that feed upon or decompose the producers.

Community Characteristics

Since the aim of the study was to measure productivity of representative populations adjusted to particular environments, microcosms were seeded with a variety of organisms. Part of the seed came directly from pond water used as a medium and part from a culture developed from other ponds. The microecosystems included algae, bacteria, protozoans, rotifers and small crustaceans. Principal algae present in the microcosms are listed in Table IV.

TABLE IV

GENERA OF ALGAE IDENTIFIED IN STABILIZED MICROECOSYSTEMS

Scenedesmus
Microcystis
Tetrahedron
Pediastrum
Vaucheria
Pandorina
Staurastrum
Coelastrum
Euglena
Spirogyra
Chlamydomonas
Cerasterias
Fragillaria
Volvox
Euastrum
Ankistrodesmus
Navicula
Chlorella
Mougeotia
Eudorina
Ulothrix
Oscillatoria
Nitzschia
Merismopedia
Closterium

Analysis of stabilized communities under the 64 sets of environmental conditions was made at the termination of experiments. Composition of the community in any microcosm was dictated by ability of organisms to succeed under the parameters established for that microcosm.

Communities were analyzed and compared on the basis of diversity. Several indices of diversity have been devised (Odum, Canlon and Kornicker, 1960). Yount (1956) and Odum, et al. (1960) have used a species diversity index:

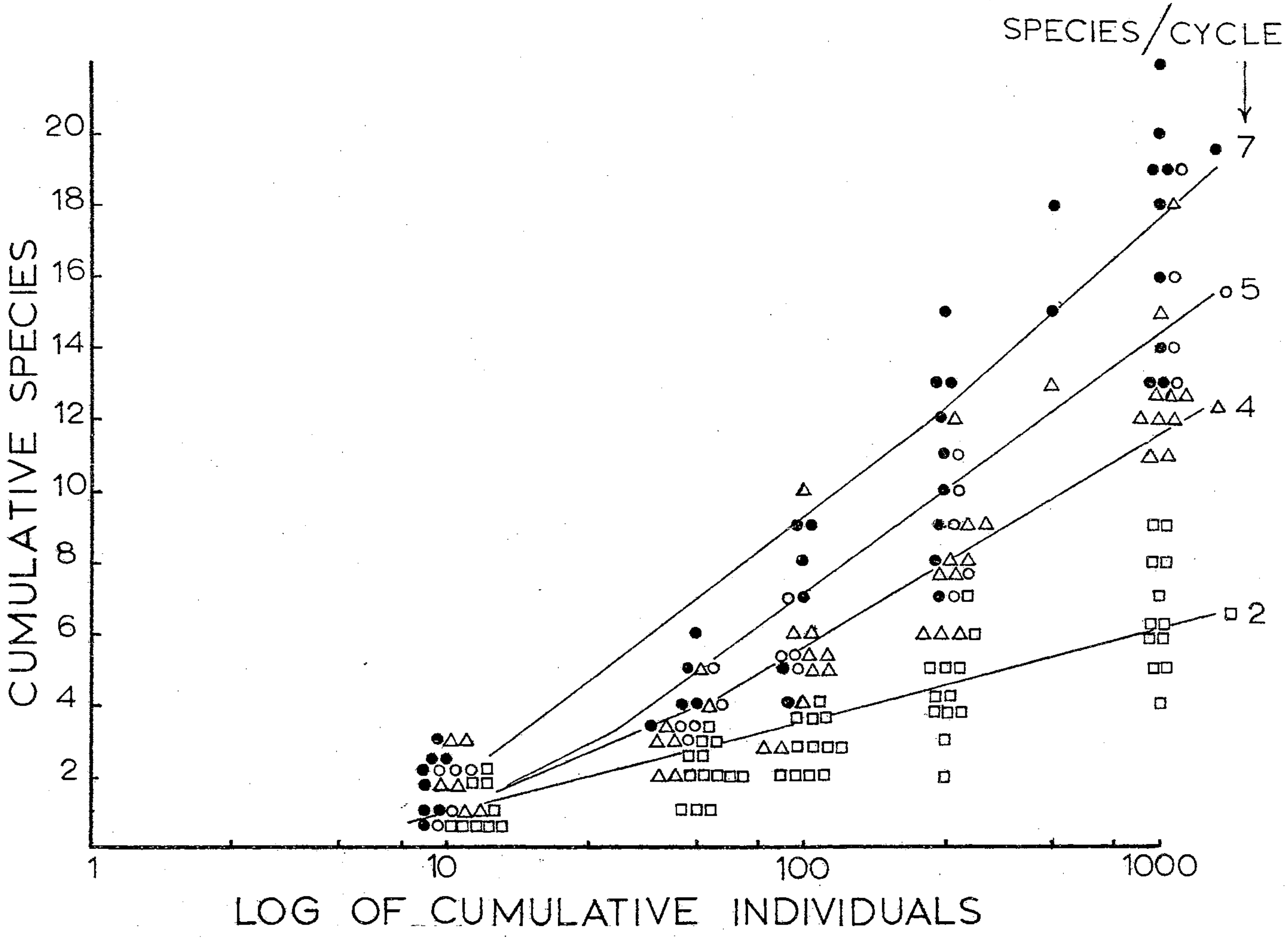
$$\text{Species Diversity} = \frac{\text{Cumulative Number of Species}}{\text{Log of Cumulative Number of Individuals}}$$

In practice, cumulative number of species is plotted against cumulative number of individuals on semilog paper and results are expressed as mean species per cycle. Straight lines may be drawn that approximate the plots and comparisons of diversity may be made on the basis of slope of the lines.

Species diversity in microcosms varied only with dissolved solids content of the water (Fig. 8). Diversity was maximum at 300 ppm with approximately seven species per cycle. At 150 ppm diversity was about five species per cycle, at 75 ppm about four species per cycle and at 600 ppm about two species per cycle. Species diversity was inhibited by high dissolved solids concentration.

Odum, et al. (1960) reported diversity of approximately three, seven and 12 species per cycle in three marine environments of different salinity. Low diversity occurred in a hypersaline bay, medium diversity in a hyposaline bay and greatest diversity in normal marine waters. A similar pattern occurred in the present study. Diversity was related to concentration of solids although absolute concentration was very different from that of Odum, et al. Low diversity in the present study was at the highest concentration of dissolved solids, second lowest diversity was at the lowest TDIS, and greatest diversity was at intermediate levels of TDIS. Highest diversity level in both the marine and microcosm environments was at intermediate and more optimal concentrations of dissolved solids.

Overall diversity in the present study ranged from two to seven species per cycle, while Beyers (1962a) reported diversity of four to seven in microecosystems. Beyers cited similarity of species diversity between microecosystems and macroecosystems as justification for



△ = 75 ppm
○ = 150 ppm
● = 300 ppm
□ = 600 ppm

Fig. 8. Species Diversity in Microcosms.

considering microecosystems as real miniatures. Similarity of effect by dissolved solids on diversity in marine and experimental ecosystems provides further evidence that microecosystems are genuine miniatures.

Programmed Integrations of Carbon Dioxide Diurnal Curves

Diurnal curves of pH were converted to carbon dioxide curves and productivity was estimated by computer.[1] The computer program, M2 UTEX PRBYPH, "Productivity Measurements by pH," was used (Armstrong, 1963).

The method consisted of two main steps. First, concentration of carbon dioxide was calculated for each pH value in a 24-hour sequence of pH readings taken at two-hour intervals in a microcosm. From a titration curve relating carbon dioxide content to pH for a particular water sample, pH-CO_2 values were read into the computer. The computer interpolated the appropriate carbon dioxide concentration for each pH, and computed the increment of change in carbon dioxide content for successive pH values. Second, the computer integrated the increments over the time period that microcosms were exposed to light and darkness and obtained net productivity and night respiration (ibid).

Similar computation may be done by hand. A titration curve is drawn from pH changes obtained by addition of carbonic acid (demineralized water saturated with gaseous carbon dioxide) to the microcosm water. Amount of change in carbon dioxide content between two successive pH values in a diurnal sequence is read from the curve and plotted

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[1] Control Data Corporation 1604 Digital Computer, Computation Center, University of Texas.

against time. A 24-hour graph is prepared (Fig. 4) which may be integrated by planimetry to obtain productivity and respiration.

The computer program calculated net productivity and night respiration. Gross productivity and total community respiration were computed by hand on the assumption that night respiration may be used as an estimate of respiration during the day. Since night and day periods were of equal length, gross productivity = net productivity + night respiration and total respiration = 2 x night respiration. Appendix A contains the values for net and gross productivity as well as night and total respiration for 356 diurnal curves of pH.

Carbon Dioxide Metabolism

Mean values calculated for both net or apparent productivity and gross or total productivity are shown in Tables V and VI. Difference between net and gross productivity represents photosynthate oxidized in respiration. Mean total respiration is presented in Table VII and is two times respiration during either light or darkness since 12-hour periods of each were used.

If phenomena occurring in microcosms are the same as in natural ecosystems, productivity in microcosms should have some relationship to that in ponds. The approximate range of gross primary productivity was 0.1 to 1.0 mM CO_2/L/day. If an intermediate productivity value of 0.5 mM CO_2/L/day is converted to an areal basis, the result is 4.6 g/m^2/day of carbon dioxide assimilated. This is within the range of productivity found in ponds although productivity in microcosms was obtained at lower light intensity (cf Chapter V, Tables II and III).

Beyers (1962) found that productivity in replicate microecosystems

TABLE V

NET PRIMARY PRODUCTIVITY IN MILLIMOLES CO_2/L/DAY IN MICROCOSMS

		Light Intensity = 800 ft-c				Light Intensity = 400 ft-c			
	TDIS in ppm	Turbidity in ppm				Turbidity in ppm			
		0	25	50	75	0	25	50	75
Temperature 23 C	075	.179	.236	.231	.163	.196	.171	.144	.129
	150	.377	.319	.250	.216	.191	.090	.115	.084
	300	.489	.278	.326	.278	.199	.131	.124	.103
	600	.234	.213	.135	.133	.101	.069	.052	.053
Temperature 11 C	075	.129	.100	.119	.126	.131	.112	.097	.125
	150	.197	.189	.202	.180	.199	.174	.091	.088
	300	.337	.277	.287	.216	.220	.197	.123	.113
	600	.119	.111	.081	.065	.060	.037	.055	.059

TABLE VI

GROSS PRIMARY PRODUCTIVITY IN MILLIMOLES CO_2/LITER/DAY IN MICROCOSMS

		Light Intensity = 800 ft-c				Light Intensity = 400 ft-c			
	TDIS in ppm	Turbidity in ppm				Turbidity in ppm			
		0	25	50	75	0	25	50	75
Temperature 23 C	075	.387	.497	.476	.334	.415	.354	.281	.269
	150	.654	.500	.417	.382	.338	.154	.192	.144
	300	.855	.556	.581	.515	.387	.268	.255	.220
	600	.468	.420	.271	.262	.198	.135	.103	.094
Temperature 11 C	075	.274	.230	.260	.263	.272	.246	.211	.233
	150	.377	.319	.416	.392	.389	.281	.165	.168
	300	.652	.560	.557	.409	.422	.375	.290	.215
	600	.217	.216	.161	.129	.126	.079	.106	.115

TABLE VII

MEAN TOTAL DAILY RESPIRATION IN MILLIMOLES CO_2/LITER/DAY IN MICROCOSMS

		Light Intensity = 800 ft-c				Light Intensity = 400 ft-c			
	TDIS in ppm	Turbidity in ppm				Turbidity in ppm			
		0	25	50	75	0	25	50	75
Temperature 23 C	075	.416	.522	.422	.341	.428	.366	.274	.256
	150	.553	.430	.418	.330	.294	.129	.182	.120
	300	.731	.556	.510	.473	.335	.313	.262	.234
	600	.466	.416	.272	.257	.194	.132	.101	.082
Temperature 11 C	075	.289	.259	.282	.275	.282	.266	.227	.216
	150	.378	.319	.430	.422	.362	.214	.164	.168
	300	.633	.566	.521	.385	.369	.355	.296	.204
	600	.198	.192	.144	.129	.131	.083	.104	.109

ranged from 0.579 to 0.846 mM CO_2/L/day for ecosystems exposed to energy sources of 203 to 380 Kcal/m^2/day. Values obtained in the present investigation were generally less, but of the same order of magnitude, and energy available for photosynthesis was somewhat less. McConnell (1962) reported gross photosynthesis of 0.86 to 1.69 g O_2/m^2/day in seven microcosms in which productivity was related to amounts of inorganic nutrients added. His productivity values were lower than most values in the present study. McConnell's microcosms were exposed through a laboratory window to natural light with a maximum noon intensity of 4000 foot candles.

Carbon dioxide concentration at any time was the product of activities by all organisms present in the microecosystem, primarily by respiration of all forms and use of carbon dioxide by algae during the day. Algae also are capable of carbon dioxide fixation in the dark and some bacteria are known to fix carbon dioxide (Bonner, 1950). Other aquatic organisms may fix carbon dioxide to an appreciable extent (Hammen, 1962). Estimates of primary productivity based on diurnal fluctuations of carbon dioxide concentration may be biased upward because of nonphotosynthetic fixation. Respiration estimates may be biased downward because carbon dioxide release during respiration may be counteracted by carbon dioxide removal from the water by dark fixation.

Potential variation in productivity measurements as a result of nonphotosynthetic fixation of carbon dioxide was estimated by comparison of $carbon^{14}$ uptake by microcosm organisms in light and darkness. Dark fixation in four microcosms ranged between 10 and 21% of light fixation by replicate samples from mature communities taken at the termination of productivity studies.

Ratio of Productivity to Respiration

P/R ratios divergent from unity over a long period of time are characteristic of ecosystems with import, export or storage. Ratios in excess of one must be balanced in time by ratios less than one in closed systems. Mean ratios of productivity to respiration approached unity in the microecosystems (Table VIII). P/R ratios fluctuated from week to week during the experimental period. However, most variations from unity were of insignificant value and overall P/R ratio was sufficiently close to one to indicate that the microecosystems were closed systems. Where significant variation occurred, no pattern coinciding with environmental variables could be detected.

Communities were allowed to stabilize about three weeks before sampling was begun. Extreme P/R ratios were obtained in a few microcosms on the initial sampling date, indicating that communities were still stabilizing. These values (starred in Appendix A, Table II) were not included in computation of means.

Oxygen Metabolism

Productivity and respiration were measured from diurnal changes in oxygen concentration in eight microcosms (Table IX). Estimates from oxygen and carbon dioxide concentrations differed in some cases by a factor of nearly two. Ratio of oxygen produced to carbon dioxide assimilated on a mole for mole basis is the photosynthetic quotient (PQ). Values of PQ are dependent on the types of compounds produced by organisms, viz. proteins, fats and carbohydrates. Community measurements of

TABLE VIII

MEAN RATIO OF GROSS PRODUCTIVITY TO TOTAL COMMUNITY RESPIRATION (P/R RATIO) IN MICROCOSMS

	Light Intensity = 800 ft-c					Light Intensity = 400 ft-c			
	TDIS in ppm	Turbidity in ppm				Turbidity in ppm			
		0	25	50	75	0	25	50	75
Temperature 23 C	075	.93	.96	1.20	.99	.97	.97	1.02	1.09
	150	1.27	1.16	.99	1.16	1.16	1.21	1.04	1.26
	300	1.21	1.00	1.18	1.10	1.18	.86	.97	.93
	600	1.04	1.02	1.01	1.05	1.07	1.07	.90	1.18
Temperature 11 C	075	.96	.89	.93	.96	.97	.94	.92	1.08
	150	1.00	1.01	1.02	.92	1.08	1.50	1.02	.98
	300	1.02	1.03	1.34	1.13	1.19	1.07	.96	1.08
	600	1.16	1.21	1.16	1.03	.97	.96	1.04	1.08

TABLE IX

OXYGEN METABOLISM AND PHOTOSYNTHETIC QUOTIENTS IN EIGHT MICROCOSMS

Microcosm Number	Combination of Environmental Variables	mM O_2/L/Day				mM CO_2/L/Day	PQ
		Net P	Gross P	Night R	Total R	Gross P	
6	Low Light, High Temp. 300 ppm TDIS, 50 ppm Turbidity	.122	.266	.144	.288	.416	.64
12	High Light, High Temp. 150 ppm TDIS, 75 ppm Turbidity	.119	.330	.211	.422	.358	.92
15	High Light, High Temp. 300 ppm TDIS, 50 ppm Turbidity	.136	.292	.156	.312	.432	.68
21	High Light, Low Temp. 300 ppm TDIS, 0 ppm Turbidity	.202	.488	.286	.592	.733	.67
34	Low Light, High Temp. 600 ppm TDIS, 50 ppm Turbidity	.171	.280	.109	.218	.144	1.94
46	High Light, High Temp. 75 ppm TDIS, 25 ppm Turbidity	.812	1.244	.432	.864	.735	1.69
52	High Light, Low Temp. 600 ppm TDIS, 75 ppm Turbidity	.245	.341	.096	.192	.218	1.56
61	Low Light, Low Temp. 75 ppm TDIS, 0 ppm Turbidity	.218	.343	.125	.250	.293	1.17

PQ = Photosynthetic Quotient
Net P = Net Primary Productivity
Gross P = Gross Primary Productivity
Night R = Night Respiration
Total R = Total Daily Respiration

photosynthetic quotient do not necessarily reflect compounds produced since many kinds of organisms, both producing and respiring, may be in different metabolic states. Ryther (1956) reviewed methods for determination of PQ, reported values for planktonic populations and suggested 1.25 as a more realistic PQ than unity. Park, Hood and Odum (1958) reported a range of PQ of 0.3 to 1.0 in shallow marine bays. Values in the present study were between 0.6 and 1.9. Higher values were associated with oxygen concentrations in excess of saturation and lower values were associated with concentrations well below saturation throughout most of the day. Photosynthetic quotients divergent from theoretical ones may have resulted as much from imperfect diffusion corrections as from metabolic differences between ecosystems.

Chlorophyll and Biomass

Standing crop or biomass may be estimated by volume measurements, ash-free dry weight or chlorophyll concentration (Verduin, 1956). Volume measurements require tedious and time-consuming counts followed by multiplication with standard volume-weight factors of uncertain accuracy. Ash-free dry weight estimates were preferred for weekly studies because smaller samples (50 ml) of microcosm water were required as compared to samples for chlorophyll estimates (100 ml).

Mean ash-free dry weight for samples from the 64 microcosms is shown in Table X. Biomass was affected by mineral concentration of water but there was no significant effect by differences in turbidity, temperature or light intensity.

At termination of the studies, chlorophyll extractions were made on 100 ml samples of microcosm water. Concurrently samples were treated

TABLE X

BIOMASS AS MEAN ASH-FREE DRY WEIGHT IN G/L. IN MICROCOSMS

		Light Intensity = 800 ft-c				Light Intensity = 400 ft-c			
	TDIS in ppm	Turbidity in ppm 0	25	50	75	Turbidity in ppm 0	25	50	75
Temperature 23 C	075	.170	.229	.154	.177	.122	.173	.128	.104
	150	.230	.240	.246	.180	.190	.140	.157	.176
	300	.406	.460	.410	.323	.289	.296	.282	.286
	600	.593	.533	.540	.574	.547	.536	.525	.510
Temperature 11 C	075	.126	.105	.133	.130	.145	.127	.121	.109
	150	.238	.244	.201	.199	.178	.170	.179	.158
	300	.310	.303	.313	.292	.278	.285	.266	.248
	600	.494	.526	.512	.515	.511	.551	.515	.504

to determine ash-free dry weight. Correlation coefficients ($r = \frac{\Sigma xy}{\sqrt{\Sigma x^2 \Sigma y^2}}$) were determined separately for sixteen microcosms at each of the four turbidity and TDIS levels. Correlation between chlorophyll and ash-free dry weight was greatest with no turbidity and least at the highest turbidity. Coefficients were 0.54 at 0 ppm turbidity, 0.47 at 25 ppm, 0.25 at 50 ppm, and 0.21 at 75 ppm. When microcosms were compared by TDIS level, higher correlation was found at the two higher levels. Correlation coefficients for all levels were: 0.29 at 75 ppm TDIS, 0.38 at 150 ppm, 0.79 at 300 ppm and 0.72 at 600 ppm. Chlorophyll and ash-free dry weight were most closely related at high TDIS and low turbidity. Less non-producer biomass was present at high ionic content and low turbidity. In such situations, ratio of gross productivity to biomass was uniformly low (Table XI). It appeared that sufficient chlorophyll was present at high TDIS levels for the high biomass concentrations to be more productive than the low levels recorded (Tables VI, X and XI). 600 ppm TDIS was inhibitory to production since chlorophyll appeared to be less active than at lower concentrations of TDIS.

Pigment extracts from a group of **nine** microcosms were used to compare community concentrations of the following pigments: chlorophylls a, b and c and astacin and non-astacin type carotenoid pigments (Table XII). Concentrations of the five pigment types were converted to per cent of each type with the total as 100 per cent. Chlorophyll c and carotenoid pigment concentrations obtained by the method of Richards and Thompson (1952) are in MSPU (thousandths of the arbitrary Specific Pigment Unit). MSPU is approximately equal to 1 mg pigment since the SPU is theoretically equal to one gram pigment for which the absorption spectrum is not known. Concentration of chlorophylls a and b and total

TABLE XI

CHLOROPHYLL CONCENTRATION IN MG/L IN MICROCOSMS

		Light Intensity = 800 ft-c				Light Intensity = 400 ft-c			
	TDIS in ppm	Turbidity in ppm				Turbidity in ppm			
		0	25	50	75	0	25	50	75
Temperature 23 C	075	.520	1.329	.549	.590	.467	1.744	1.359	.838
	150	.637	.778	1.187	1.751	.778	.353	.465	.346
	300	3.341	5.376	2.630	1.574	2.112	1.313	2.557	3.245
	600	3.611	2.105	1.225	2.118	.910	1.321	1.489	1.097
Temperature 11 C	075	.373	.675	.423	.538	.721	.409	.354	.664
	150	1.027	1.352	1.498	.799	1.114	1.137	.822	.603
	300	1.670	3.533	1.866	1.067	1.202	1.862	1.444	1.759
	600	.856	.597	.419	.414	.445	.388	.327	.304

TABLE XII

CONCENTRATION AND PERCENT CONCENTRATION OF CHLOROPHYLLS a, b, AND c AND ASTACIN AND NON-ASTACIN TYPE CAROTENOID PIGMENTS IN NINE MICROCOSMS AT 11 C AND 400 FT-C; 13' WAS AT 23 C AND 800 FT-C

Microcosm Number	Turbidity ppm	TDIS	Chlorophyll a		Chlorophyll b		Chlorophyll c		Astacin		Non-astacin		Total
			mg/L	%	mg/L	%	mg/L	%	mg/L	%	mg/L	%	mg/L
57	0	600	.445	21.2	.188	8.9	1.286	61.1	.145	6.9	.040	1.9	2.104
58	25	600	.388	37.5	.064	6.2	.434	41.9	.061	5.9	.088	8.5	1.035
59	50	600	.327	33.2	.065	6.6	.463	47.1	.082	8.3	.047	4.8	.984
60	75	600	.304	43.4	.036	5.1	.219	31.2	.038	5.4	.104	14.8	.701
13'	0	300	2.116	58.3	.246	6.78	.180	5.0	*	0.0	1.085	29.9	3.627
61	0	75	.721	40.9	.121	6.9	.594	33.7	.042	2.4	.283	16.1	1.761
62	25	75	.409	34.3	.075	6.3	.510	42.8	.054	4.5	.144	12.1	1.192
63	50	75	.354	70.3	.005	0.99	*	0.0	.0004	0.08	.144	28.6	.503
64	75	75	.664	65.4	.007	0.69	*	0.0	*	0.0	.345	34.0	1.016

* Negative value, added in as zero.

pigments varied inversely with turbidity except in microcosm 64. Significant differences between the two extremes of TDIS in total pigments and chlorophyll a were not evident. At 600 ppm TDIS, concentration of astacin type carotenoids was distinctly higher than at 75 ppm. Astacin carotenoids are characteristic of crustaceans (ibid), thus the observed concentrations may reflect the number of crustaceans in the microcosms. Large numbers of copepods were observed on many occasions in the 600 ppm microcosms. The pigment method used is susceptible to error in estimating chlorophyll c. Negative results obtained with microcosms 63 and 64 possibly were caused by error in the method.

Productivity Per Unit Biomass

Historically, measurement of change in biomass or standing crop of producer organisms was the first approach to production studies. This method is suitable for many habitats but is of little value in aquatic situations. Much primary production may be removed by grazing organisms and is not subject to biomass measurements, and biomass measurements give no indication of short-term rates of formation (Ryther, 1956; Goldman, 1960). Recent productivity studies have been based on rate of uptake or release of one of the reactants of photosynthesis and respiration. Production rates thus obtained are little affected by grazing. Some investigators have indicated rate of production with no measure of biomass (Odum and Hoskin, 1958; Weber, 1958; Copeland, et al., 1962). Other investigators have computed short-term photosynthetic yield per unit of standing crop (Verduin, 1956; Wright, 1959, 1960; Hepher, 1962). In many cases the most useful data consist of productivity per unit of producer biomass per unit of radiation. Strickland

(1960) refers to this ratio as "productivity index." Comparison of fertility of various water bodies requires productivity and biomass measurements in order to distinguish between large biomasses photosynthesizing at low rates and small biomasses photosynthesizing at vigorous rates. Ryther (1960) has pointed out the fallacy of comparing productivity by phytoplankton with a rapid recycling rate to productivity that results in accumulation of a harvestable biomass.

Producer biomass is not readily distinguished from total biomass. Chlorophyll content of producers has been used as an estimate of such biomass but may include appreciable quantities of nonfunctional chlorophyll (Strickland, 1960). For calculating productivity per unit of biomass, ash-free dry weight was used as an estimate of biomass. Consumer and decomposer biomass was included as well as active and moribund producers.

Ratio of gross productivity in milligrams to biomass in grams varied between 0.087 and 8.232 (Appendix A). No pattern of fluctuation in ratio with successive weekly samples occurred but irregular and notable fluctuations did occur. Distinct differences were obvious in the mean ratios of productivity to biomass (Table XIII). Ratios were higher at 23 C than at 11 C with high light intensity but differences were minimal at low light intensity. Most apparent variation was in response to TDIS level. Considering all microecosystems at the appropriate concentrations, productivity per unit biomass was greatest at the lowest concentration of TDIS. Ratios were similar in value for 150 and 300 ppm and decreased by two-thirds or more with doubling of TDIS from 300 to 600 ppm. Variation in ratio with increase in turbidity was not consistent throughout the range of experimental conditions.

TABLE XIII

GROSS PRODUCTIVITY PER UNIT OF BIOMASS IN MG/G

		Light Intensity = 800 ft-c				Light Intensity = 400 ft-c			
	TDIS in ppm	Turbidity in ppm				Turbidity in ppm			
		0	25	50	75	0	25	50	75
Temperature 23 C	075	3.19	2.52	3.68	2.30	4.16	2.32	2.30	2.79
	150	3.00	2.49	1.87	2.29	1.92	1.16	1.24	.89
	300	2.14	1.40	1.76	1.64	1.37	.93	.91	.78
	600	.77	.79	.50	.46	.36	.26	.21	.18
Temperature 11 C	075	2.24	2.33	2.17	2.26	2.09	2.06	1.99	2.18
	150	1.59	1.43	2.15	1.72	1.97	1.75	1.00	.97
	300	1.96	1.85	1.80	1.52	1.32	1.29	1.02	.90
	600	.44	.42	.32	.26	.27	.15	.23	.25

Turbidity appeared to affect ratio of productivity to biomass at the higher temperature and more so at higher TDIS levels than at lower. The pattern of variation in ratios is similar to the pattern for gross productivity (Table VI), a fact that might well be expected since biomass varies only minimally with factors other than TDIS.

Assimilation number for an ecosystem reflects the relationship that exists between productivity and producer biomass. Assimilation number was computed as mg oxygen produced per hour per mg chlorophyll a, assuming a photosynthetic quotient of 1.25 (Table XIV). Conversion of carbon dioxide data to oxygen was performed to make present data comparable to that in the literature. Since assimilation is associated with gross photosynthesis (Odum, et al., 1958), values for gross productivity were used.

Assimilation numbers ranged from 0.4 to 4.0 in contrast to 0.02 to 4.0 reported by Odum, et al. and 1.0 to 13.8 reported by Copeland (1963). The pattern of assimilation number in relation to environmental variables was irregular and dissimilar to that for productivity or productivity per unit biomass. As light intensity increases, assimilation number increases and chlorophyll content decreases (Odum, et al., 1958). No apparent variation occurred in response to light intensity or turbidity in the present study. Light saturation occurred only at the lowest TDIS concentration, therefore, it appeared that light intensities used were less than necessary to cause variation in assimilation number. As in the case of productivity/biomass ratio, assimilation number was more closely associated with TDIS concentration than other environmental factors. At high temperature, assimilation number decreased as TDIS concentration increased. At low temperature, assimilation numbers were

TABLE XIV

ASSIMILATION NUMBERS FOR MICROECOSYSTEMS

		Light Intensity = 800 ft-c				Light Intensity = 400 ft-c			
	TDIS in ppm	Turbidity in ppm				Turbidity in ppm			
		0	25	50	75	0	25	50	75
Temperature 23 C	075	2.25	2.54	4.10	2.74	3.22	.85	1.07	1.69
	150	2.14	2.56	1.44	1.15	1.58	2.30	1.89	2.36
	300	1.10	.45	.83	1.32	.74	1.05	.47	.31
	600	.71	1.65	1.22	.84	1.16	.56	.44	.48
Temperature 11 C	075	3.97	1.20	2.98	1.96	1.86	2.68	1.01	1.28
	150	1.76	1.06	1.37	2.68	1.76	1.21	1.32	1.25
	300	1.64	.75	2.23	2.08	1.53	.81	1.34	.71
	600	2.68	2.59	2.74	2.41	2.67	1.58	2.69	2.97

slightly lower at intermediate TDIS levels and higher at the extremes.

CHAPTER VII

ANALYSIS OF EXPERIMENTAL DATA

Metabolic processes are limited in rate by the essential reactant present in smallest quantity relative to minimal requirement. This statement may be expanded to include physical ecological factors such as light and temperature (Stumm and Morgan, 1962). Complex processes like community photosynthesis may be controlled by interaction of several factors. The limiting factor for community photosynthesis is related to other factors and is best expressed in terms of levels of related factors. Ecological factors may be limiting at maximal as well as minimal levels. Light intensity may be sufficiently high to become rate inhibitory to photosynthesis when photooxidation begins.

Experiments reported here were designed to be analyzed in a manner that not only measures effects of individual factors but also measures effects of factor interactions. In a factorial experiment all possible combinations of the levels of experimental factors are tested. In this study 64 combinations were required by four levels of turbidity, four levels of TDIS, two temperatures and two light intensities (4 x 4 x 2 x 2). Statistical and informational advantages arise from the factorial method as compared to classical experimental methods in which all factors but one are held constant (Fisher, 1937; Bailey, 1959). These advantages as summarized from the work of Fisher and Bailey are:

(1) A wider spectrum of information is obtained since interactions

are evaluated as well as single factors. If the factors are independent, as much information is obtained about each factor as if the factor had been treated independently.

(2) Greater efficiency results since factors may be evaluated with fewer observations than would be necessary if the factors were studied singly.

(3) A wider basis for inference about factors is obtained when the factors are studied under a variety of conditions. The potential for practical application is enhanced.

A statement by Fisher (1926) is pertinent to research with experimental ecosystems.

> No aphorism is more frequently repeated in connection with field trials, than that we must ask Nature few questions, or, ideally, one question, at a time. The writer is convinced that this view is wholly mistaken. Nature, he suggests, will best respond to a logical and carefully thought out questionnaire; indeed, if we ask her a single question, she will often refuse to answer until some other topic has been discussed.

Effects caused by action of a single factor are main effects. Effects that are either more or less than simple addition of more than one main effect are interactions. Interactions of two factors are first-order interactions, of three factors are second-order interactions, and of four factors are third-order interactions. Interpretation becomes more difficult as the order of interaction increases.

An analysis of variance was made (Table XV) and significance of main effects and interactions was tested by experimental error. The error term was obtained by lumping effects for third-order interactions. Use of third-order interactions as an error term assumes that these interactions are not real; however, it is possible for one or more to be real. Other interactions or even main effects frequently are null, and

TABLE XV

ANALYSIS OF VARIANCE FOR MEAN GROSS PRODUCTIVITY IN MICROCOSMS

Source	df	Sum of Squares	Mean Square	F
A Main Effect	3	0.176182	0.058727	19.71 **
B	3	0.506899	0.168966	56.71 **
C	1	0.473861	0.473861	159.03 **
D	1	0.079595	0.079595	26.71 **
A x B Interaction	9	0.046319	0.005146	1.73
A x C	3	0.003119	0.001039	0.35
A x D	3	0.016438	0.005479	1.84
B x C	3	0.108941	0.036314	12.19 **
B x D	3	0.032374	0.010791	3.62
C x D	1	0.064325	0.064325	21.59 **
A x B x C	9	0.028634	0.003182	1.07
A x B x D	9	0.022655	0.002517	0.85
A x C x D	3	0.010952	0.003651	1.23
B x C x D	3	0.003757	0.001252	0.42
A x B x C x D	9	0.026817	0.002979	
TOTAL	63	1.600868		

theoretically ought to be included in the error term. An alternative procedure for determination of significance as suggested by the data is the use of half-normal graphs.

Contrasts or comparisons for all combinations of factors may be made. Each contrast has a single degree of freedom associated with it and the sum of the degrees of freedom for separate contrasts is equal to the total degrees of freedom for experimental treatments. One less than the total number of treatments is the number of contrasts that can be made. In this study 63 contrasts were made between combinations of factors (Appendix B). Comparisons are independent of one another and are termed an orthogonal set (Steel and Torre, 1960). Effect of any one of the members of the set was computed from:

$$\text{Effect} = \frac{Q}{\sqrt{K}}$$

Where $Q = \sum c_i T_i$ = sum of coefficients times treatment means.

$K = \sum c_i^2$ = sum of squares of coefficients of contrast.

c_i = coefficient for ith combination of factors.

T_i = mean productivity of the ith combination of factors.

Significance of effect for any member of the set of orthogonal comparisons was derived from deviation of that effect from a rank order plot of effects (Fig. 9). Effects were plotted in successive order on half-normal grid (Daniel, 1959) disregarding sign. The lowest value was plotted at one on the ordinate, second lowest at two, and so on to the highest value at 63. A line was fitted through the points by eye. Effects with greatest horizontal deviation from the line were judged most significant. Effects that fell well off the line and appeared not to be part of the error contrasts were disregarded and a second plot was constructed using 44 effects lowest in absolute value (Fig. 10).

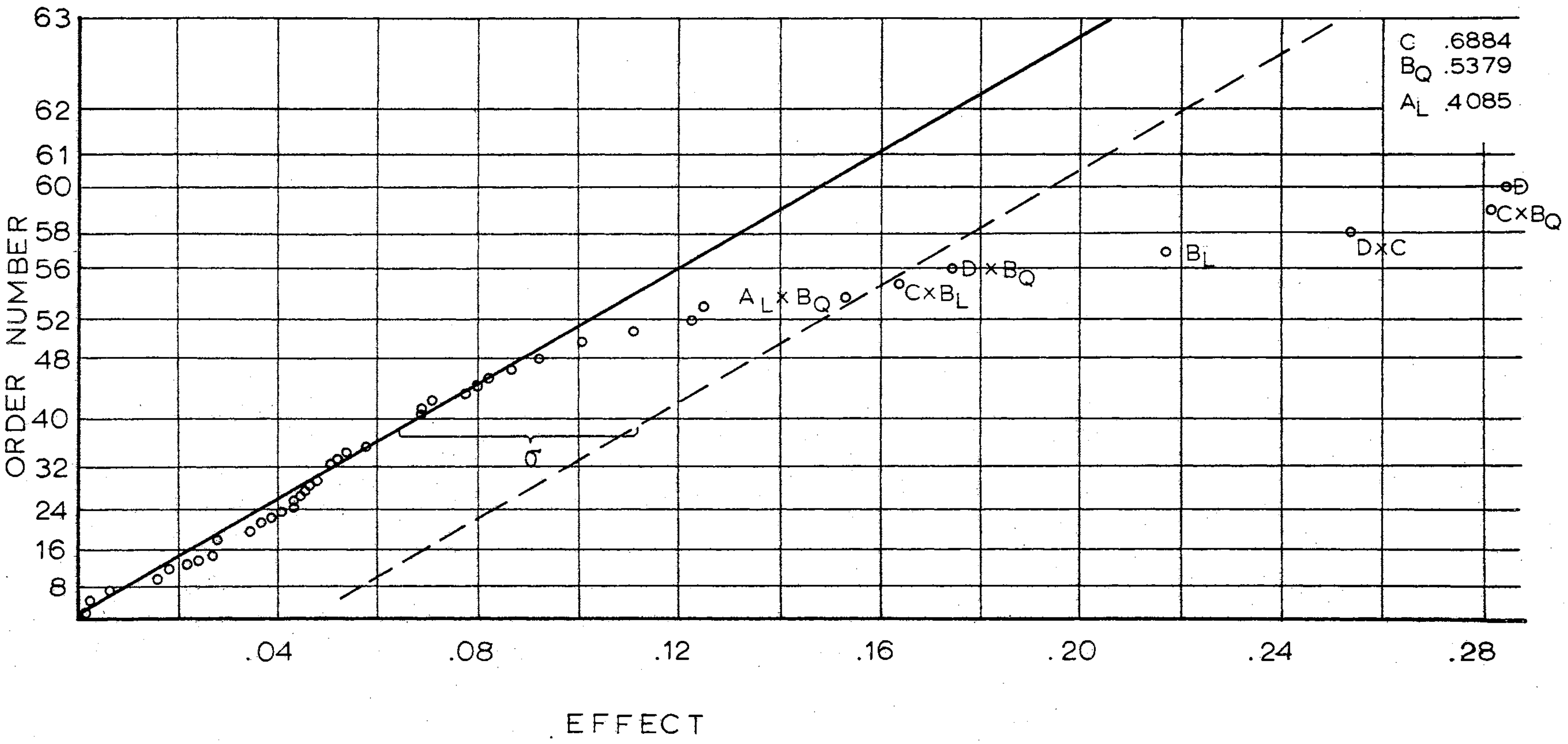

Fig. 9. Half-Normal Plot of effects by all contrasts. Values that fall on or near the solid line are part of the group of contrasts that estimate error. Dashed line indicates distance of $\tilde{\sigma}$ from the solid line. Significant effects are those identified by letters.

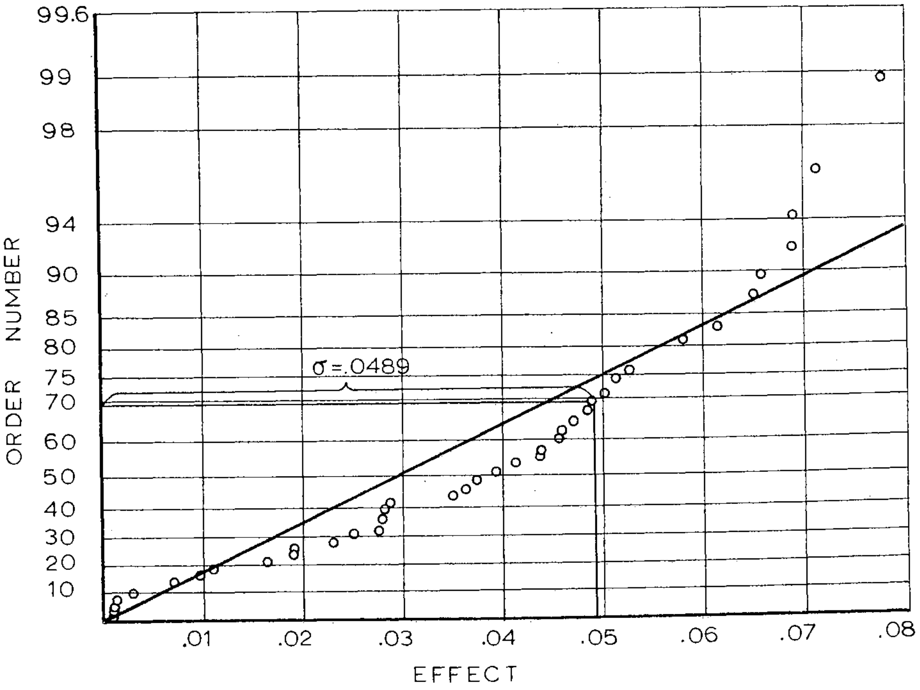

Fig. 10. Half-Normal Plot of 44 effects lowest in absolute value.

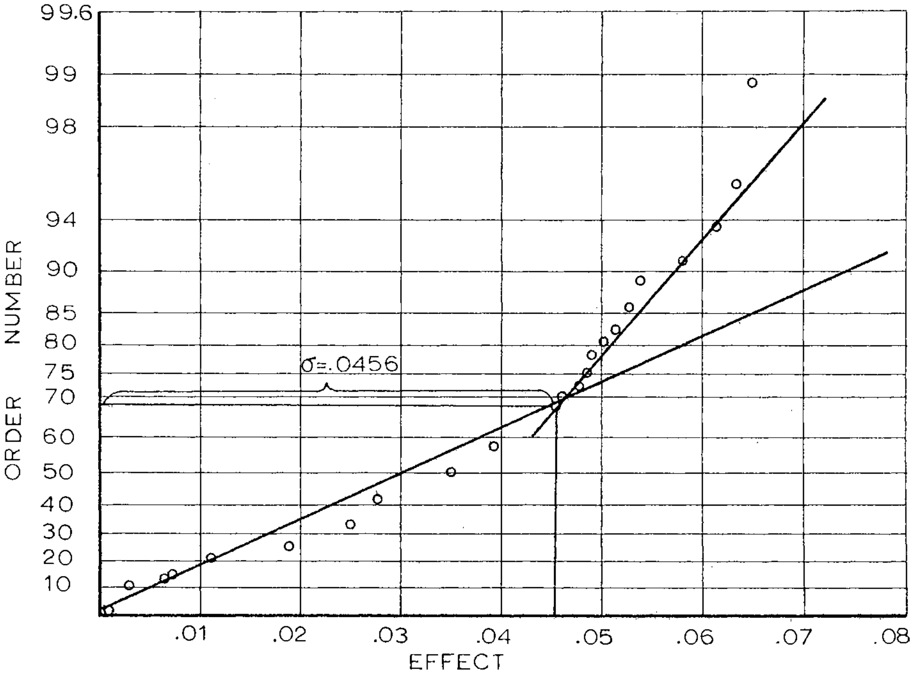

Fig. 11. Half-Normal Plot of 39 effects lowest in absolute value.

Standard deviation, σ, was estimated by using the value of the effect for which probability was nearest 0.683 (Godbey, 1963). σ from Fig. 10 was 0.0489. A third plot (Fig. 11) was constructed from the 39 effects lowest in absolute value. σ determined as above was 0.0456. Since σ from Fig. 10 was not greatly different from σ in Fig. 11, 0.0456 was used to test effects for significance. Contrasts were subjected to an F test using the error term from Table XV and σ^2 from Fig. 11 ($0.0456^2 = 0.002079$) and results are shown in Table XVI. Results from either F test were similar to those obtained by measuring the distance of σ from the line in Fig. 9.

Physical limitations of space required that experiments be run in two sets. The experiments were blocked on factor B_C, the cubic effect of total dissolved inorganic solids. Thus one set consisted of TDIS at 150 and 300 ppm and the other consisted of TDIS at 75 and 600 ppm. Effect due to B_C was lost for interpretation.

Response Surface

The entire set of results from a factorial experiment may be analyzed at once by use of a response surface (Fig. 12). The response surface depicted is essentially a graph of response or output for all combinations of factors in the experiment with responses interconnected by lines to form a surface. In the present study responses consisted of mean gross productivity and it was plotted for each combination of turbidity and TDIS to produce a response surface. For ease of reading, four surfaces were separated by temperature and light intensity. However, the four surfaces could be drawn on a single set of axes.

At any combination of light intensity and temperature, there are

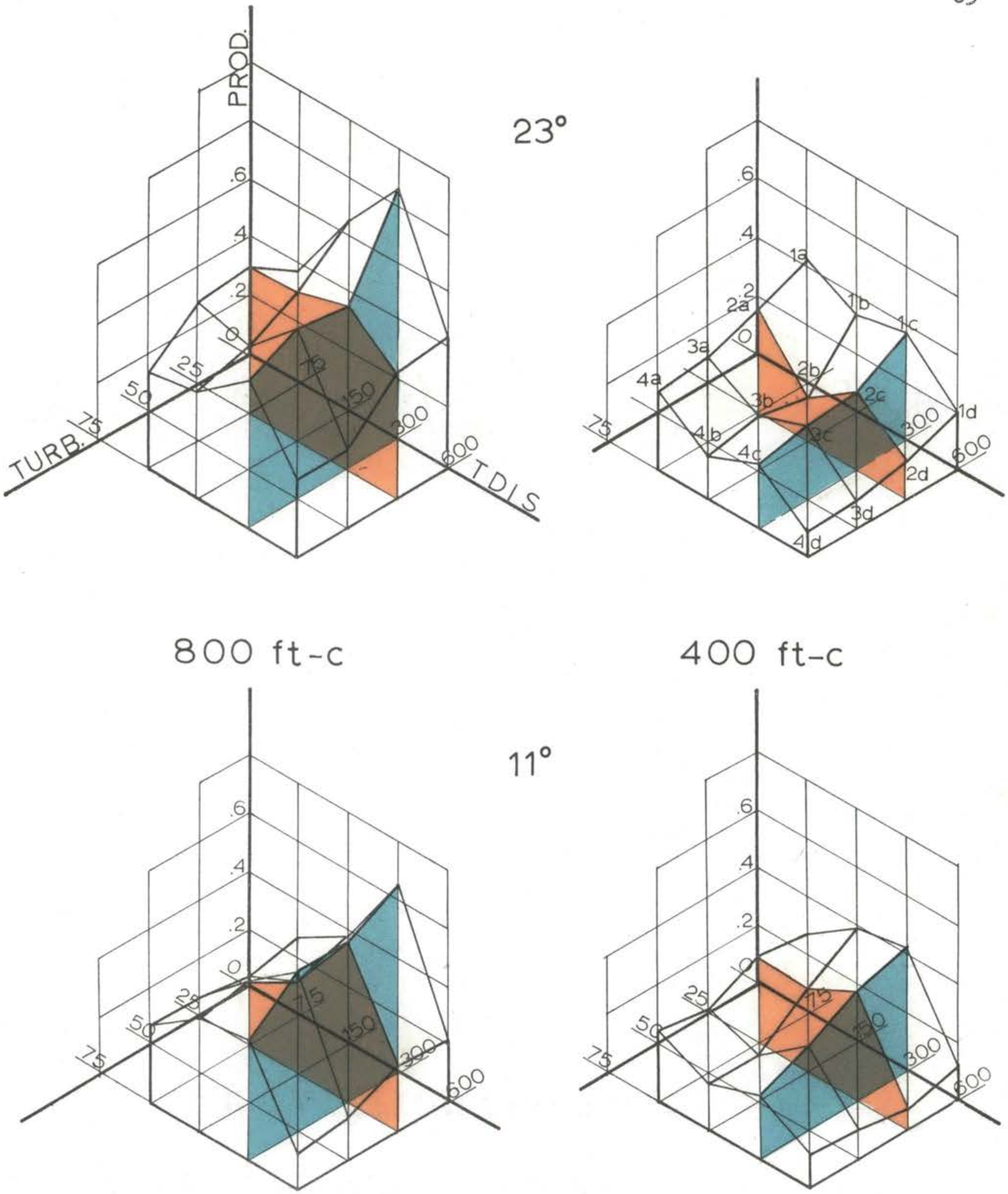

Fig. 12. Response Surface of Mean Gross Productivity for all combinations of environmental variables. Prod. = Mean Gross Productivity in mM CO_2/L/day, Turb. = Turbidity in ppm, and TDIS = Total Dissolved Inorganic Solids in ppm. Responses indicated by the same letter in the upper right drawing form a graph of response to turbidity. Responses indicated by the same number form a graph of response to TDIS. Turbidity graphs are in heavy lines, TDIS graphs in light lines.

TABLE XVI

COMPARISON OF F VALUES AND SIGNIFICANCE BASED ON MEAN SQUARE FROM THIRD-ORDER INTERACTIONS (0.002979) AND HALF-NORMAL PLOT (0.002079)

Rank	Contrast	Effect	Mean Square = 0.002980			Mean Square = 0.002079		
			F	Signif.		F	Signif.	
				.05	.01		.05	.01
1	C	0.6884	159.05	x	x	227.94	x	x
2	B_Q	.5379	97.10	x	x	139.17	x	x
3	A_L	.4085	56.00	x	x	80.27	x	x
4	D	.2821	26.70	x	x	38.28	x	x
5	B_Q x C	.2814	26.60	x	x	38.09	x	x
6	D x C	.2536	21.58	x	x	30.93	x	x
7	B_L	.2167	15.76	x	x	22.59	x	x
8	B_Q x D	.1744	10.21	x		14.63	x	x
9	B_L x C	.1605	8.64	x		12.39	x	x
10	A_L x B_Q	.1534	7.90	x		11.32	x	x
11	A_L x B_C x C	.1254	5.28	x		7.56	x	
12	A_L x D	.1229	5.07			7.26	x	
13	A_L x B_L x C	.1180	4.67			6.70	x	
14	A_L x B_Q x C x D	.1008	3.41			4.89		
15	A_L x C x D	.0927	2.88			4.13		

Signif. = Significance

four graphs of productivity versus TDIS concentration, one for each level of turbidity. Similarly there are four graphs of productivity versus turbidity, one for each concentration of TDIS. At 23 C and 400 ft-c, responses indicated by the same letter (1a, 2a, 3a, 4a) form a graph or plane of response to turbidity, in this case at 75 ppm TDIS. Responses indicated by the same number (1a, 1b, 1c, 1d) form a graph of response to TDIS, in this case at 0 turbidity. Responses to turbidity are graphed with heavy lines, responses to TDIS with light lines.

Some planes of response are difficult to visualize. Each plane of response to TDIS at 25 ppm turbidity has been indicated in orange. The planes of response to turbidity at 300 ppm TDIS have been indicated in blue. Blending of colors occurred where the planes overlap.

Effect of Environmental Factors on Productivity

Significant main effects were produced by light intensity (factor C), temperature (D), quadratic and linear effects of TDIS (B_Q and B_L), and linear effect of turbidity (A_L), cf Tables XV and XVI; Fig. 9 and Fig. 12. Significant interactions were produced by light intensity and temperature (C x D), light intensity and quadratic effect of TDIS (C x B_Q), linear effect of turbidity and quadratic effect of TDIS (A_L x B_Q), and light intensity and linear effect of TDIS (C x B_L).

The following conclusions are indicated:

(1) Productivity generally was greater at high than at low light intensity.

(2) Productivity was greater at intermediate TDIS and lower at extremes. That quadratic effects of TDIS were more significant than

linear may be seen from the parabolic shape of several TDIS graphs in Fig. 12. Optimal TDIS was 300 ppm except at the high temperature, low light combination where 75 ppm TDIS yielded greatest productivity.

(3) Turbidity alone was not an all-important factor at depths used in microcosms. Effect of turbidity on productivity displayed a linear relationship. Significance of A_L may be seen in Fig. 12 where response to turbidity at any TDIS level approximated a straight line. Turbidity was less effective at low than at high temperature. Turbidity influenced productivity at 75 ppm TDIS only at the combination of low light and high temperature. At 11 C, temperature was limiting, and at high light intensity and high temperature, TDIS concentration was limiting. These facts suggest that winter production rate may be similar in both clear and turbid ponds of low mineral content. At high light intensity, moderate turbidity (25 ppm) did not lower productivity excessively.

(4) Temperature alone (D) had a lower overall effect on productivity than light intensity (C) (F values in Table XVI). Gross productivity in stabilized microecosystems was increased about 50% by a 12 C increase in temperature. Total daily respiration was less affected by temperature. In most cases about 20% increase in respiration occurred with 12° rise in temperature. Beyers (1962) found that night respiration was nearly temperature independent over the range, 16 to 30 C. Net photosynthesis was minimally affected by 7° changes in temperature either above or below adapted temperature of 23 C.

(5) Interaction of light intensity and temperature had an important effect upon productivity. Temperature was less important at low than at high light intensity. With low light, productivity was about the same at either temperature, indicating that temperature was not limiting.

At 150 and 300 ppm TDIS, productivity was even greater at low than at high temperature. At high light intensity, temperature increase had a greater effect.

(6) Effect of TDIS was influenced by levels of other factors. Variation in effect of light intensity caused by different levels of TDIS resulted from the significant interaction, B_Q x C. Light had less effect at lowest TDIS than at the three higher concentrations. At 75 ppm TDIS and high temperature, productivity was nearly as great at low light and zero turbidity as the maximum at high light. Maximum productivity at high light occurred with turbidity at 25 and 50 ppm. Since the effect of turbidity is to reduce light intensity, light reached saturation level at some point between 400 and 800 ft-c. Light intensity greater than the saturating value inhibited productivity at low TDIS. Light saturation was not observed at other TDIS levels. Optimal productivity in surface waters of soft-water ponds may occur where there is some turbidity to reduce light penetration. Light may be optimal at some depth in clear ponds. Maximum light and dark bottle productivity and maximum oxygen concentration in Myers Lower Pond occurred at a depth of four to six feet (Butler, unpublished data). At the lower temperature and low TDIS, neither increase in light nor decrease in turbidity affected production. Apparently temperature was limiting. In this case B_Q x C and the interaction of temperature and light intensity, C x D, were involved.

(7) Linear effect of turbidity depended upon the level of TDIS (A_L x B_Q). Conversely, quadratic effect of TDIS was different at low than at upper levels of turbidity. Turbidity had minimal effect on productivity at 75 ppm TDIS and less at 600 ppm than at intermediate TDIS.

(8) A number of combinations of factors were found to have only marginal effect upon productivity. Included in this group were the second-order interactions: A_L x B_C x C, A_L x B_L x C, and A_L x C x D; the first-order interaction, A_L x D; and the third-order interaction, A_L x B_Q x C x D. An even larger number of combinations were found not to have significant effect upon productivity and included in this group were:

A_Q
A_C
A_C x B_C
A_Q x D
A_C x D
B_L x D
B_C x D
A_L x C
A_Q x C
A_C x C
B_C x C
A_L x B_L
A_L x B_C
A_Q x B_L
A_Q x B_Q
A_Q x B_C

A_C x B_L
A_C x B_Q
A_L x B_Q x C
A_Q x B_L x C
A_Q x B_Q x C
A_Q x B_C x C
A_C x B_L x C
A_C x B_Q x C
A_C x B_C x C
A_L x B_L x D
A_L x B_Q x D
A_L x B_C x D
A_Q x B_C x D
A_Q x B_Q x D
A_Q x B_C x D
A_C x B_L x D

A_C x B_Q x D
A_C x B_C x D
A_Q x C x D
A_C x C x D
B_L x C x D
B_Q x C x D
B_C x C x D
A_L x B_L x C x D
A_L x B_C x C x D
A_Q x B_L x C x D
A_Q x B_Q x C x D
A_Q x B_C x C x D
A_C x B_L x C x D
A_C x B_Q x C x D
A_C x B_C x C x D

CHAPTER VIII

SUMMARY

1. Primary productivity in some Central Oklahoma farm ponds varied inversely with turbidity and directly with concentration of dissolved minerals. Amount of turbidity and dissolved minerals in ponds is related to water exchange rate, therefore, exchange rate indirectly affects primary or photosynthetic productivity. Relative influence of turbidity and dissolved mineral concentration in control of primary production rate in ponds could not be separated.

2. Gross primary productivity in a clear pond with low rate of water exchange was two to three times that in an adjacent turbid pond with high water exchange rate. Summer productivity was about 12 g O_2/m^2/day in the clear pond as compared to about 4 g O_2/m^2/day in the turbid. Ratio of gross productivity to community respiration (P/R ratio) usually exceeded one in the clear pond and was less than one in the turbid pond which received allochthonous organic matter with runoff water. Productivity in three ponds in series in the same drainage increased downstream as both water exchange rate and turbidity decreased. Photosynthetic efficiency in pond communities increased as production rate increased and varied between 0.03 and 2.0%.

3. 64 microecosystems were established in the laboratory under controlled conditions utilizing all possible combinations of four environmental factors: two light intensities, two temperatures, four

levels of turbidity, and four concentrations of total dissolved inorganic solids (TDIS).

4. Stabilized communities in microecosystems were analyzed by species diversity. Diversity varied only with ionic content of the water. Diversity was maximal at 300 ppm TDIS with seven species per cycle and minimal at 600 ppm with two species per cycle. Diversity at 150 and 75 ppm was five and four species per cycle respectively. Variation in diversity with mineral content of water paralleled that reported for hypersaline, hyposaline and normal marine habitats. Principal producers in the microecosystems were: *Scenedesmus*, *Chlorella*, *Mougeotia*, *Spirogyra*, *Tetrahedron* and *Euglena*.

5. Primary productivity and community respiration were measured from diurnal changes in carbon dioxide. Change in carbon dioxide concentration per unit time was determined from a titration curve of carbon dioxide versus pH based on titration of microecosystem water with water saturated with carbon dioxide. Total positive and negative change in carbon dioxide concentration per day was calculated by computer.

6. Gross primary productivity in microecosystems ranged from 0.1 to nearly 1.0 mM CO_2/L/day. Community respiration values were of similar magnitude and P/R ratios approximated unity.

7. Community biomass varied from less than 100 to 600 mg/L. Biomass varied only with TDIS and averaged about 100 mg/L at 75 ppm TDIS, 200 mg/L at 150 ppm TDIS, 400 mg/L at 300 ppm TDIS, and 550 mg/L at 600 ppm TDIS. Chlorophyll concentration ranged from 0.3 to 5.0 mg/L and was not closely correlated with biomass. Gross productivity per unit biomass in mg/g varied between 0.09 and 8.2. Variation in the ratio was associated with temperature, light, dissolved solids content,

and turbidity in a manner similar to that for gross productivity.

8. Microecosystem evaluation was set up as a factorial experiment, 4 x 4 x 2 x 2. Significance of main effects and interactions was tested against an error term of third-order interactions in a standard analysis of variance. Significance of 63 contrasts including all possible main effects and factor interactions was tested by means of half-normal plots. Excellent agreement occurred between the two statistical methods. A response surface was constructed to illustrate effects of the four experimental factors.

9. Significant main effects and interactions were: light intensity, temperature, quadratic and linear effects of TDIS, linear effect of turbidity, light intensity x temperature, light intensity x quadratic effect of TDIS, temperature x quadratic effect of TDIS, linear effect of turbidity x quadratic effect of TDIS, and light intensity x linear effect of TDIS. Increase in light intensity resulted in increase in productivity except at 75 ppm TDIS where light was saturating. Temperature directly influenced productivity at the higher light intensity but very little at low light. Optimal TDIS was 300 ppm. TDIS appeared to affect productivity to the greatest extent but its effects were altered by interaction with other factors. Response of productivity to TDIS was better described as a parabolic curve than as a straight line. Turbidity was not uniformly effective in control of production rate nor as important as might be expected. It was less effective at lower temperature than at higher. At the higher light intensity, moderate turbidity did not reduce productivity excessively.

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APPENDIX A

TABLE I

MICROCOSM IDENTIFICATION

		Light Intensity = 800 ft-c				Light Intensity = 400 ft-c			
	TDIS in ppm	Turbidity in ppm				Turbidity in ppm			
		0	25	50	75	0	25	50	75
Temperature 23 C	075	45	46	47	48	40	39	38	37
	150	09	10	11	12	04	03	02	01
	300	13	14	15	16	08	07	06	05
	600	41	42	43	44	36	35	34	33
Temperature 11 C	075	53	54	55	56	61	62	63	64
	150	17	18	19	20	25	26	27	28
	300	21	22	23	24	29	30	31	32
	600	49	50	51	52	57	58	59	60

TABLE II

COMMUNITY METABOLISM IN MICROCOSMS AT WEEKLY INTERVALS

	#	TDIS	T	NET PRODUCTIVITY IN mM CO_2/L/DAY					NIGHT RESPIRATION IN mM CO_2/L/DAY					P/R RATIO (NET)				
TEMP. 23 C	01	150	75	.149	.030	.073	.079	.090	.057	.047	.046	.062	.088	2.614	.638	1.587	1.274	1.023
	02	150	50	.170	.049	.131	.125	.098	.034	.076	.095	.099	.094	5.000	.645	1.379	1.265	1.042
	03	150	25	.122	.042	.088	.097	.100	.054	.054	.058	.079	.077	2.259	.778	1.517	1.232	1.299
	04	150	00	.216	.136	.212	.226	.164	.144	.150	.177	.159	.105	1.500	.907	1.198	1.421	1.562
	05	300	75	.139	.069	.077	.139	.090	.126	.105	.086	.142	.127	1.103	.657	.895	.979	.709
	06	300	50	.101	.077	.162	.164	.117	.124	.112	.119	.158	.143	.815	.687	1.361	1.033	.818
	07	300	25	.132	.102	.126	.147	.150	.168	.133	.160	.172	.150	.786	.767	.787	.855	1.000
	08	300	00	.151	.171	.229	.260	.185	.178	.171	.234	.197	.158	.848	1.000	.979	1.320	1.171
	09	150	00	.448	.335	.359	.358	.387	.174	.293	.409	.309	.197	2.575	1.143	.878	1.159	1.964
	10	150	25	.453	.225	.279	.406	.230	.145	.209	.223	.224	.205	3.124	1.077	1.251	1.812	1.122
	11	150	50	.419	.183	.186	.307	.154	.126	.175	.194	.248	.220	3.325	1.046	.959	1.238	.700
	12	150	75	.383	.135	.132	.216	.216	.162	.133	.138	.171	.222	2.364	1.015	.957	1.263	.974
	13	300	00	.471	.422	.470	.692	.392	.210	.368	.434	.404	.412	2.243	1.147	1.083	1.713	.951
	14	300	25	.433	.390	.139	.204	.225	.239	.394	.221	.232	.306	1.812	.990	.629	.879	.735
	15	300	50	.437	.286	.245	.428	.234	.193	.370	.213	.257	.243	2.264	.773	1.150	1.665	.963
	16	300	75	.398	.109	.305	.322	.256	.215	.240	.286	.247	.196	1.851	.454	1.066	1.304	1.306
TEMP. 11 C	17	150	00	.234	.198	.156	.212	.186	.021	.198	.167	.183	.208	11.143	1.000	.934	1.158	.894
	18	150	25	.306	.164	.187	.157	.131	.024	.153	.159	.144	.182	12.750	1.073	1.176	1.084	.720
	19	150	50	.208	.169	.199	.224	.208	.115	.287	.207	.224	.241	1.809	.589	.961	1.000	.863
	20	150	75	.175	.083	.244	.164	.234	.015	.141	.214	.254	.234	11.667	.589	1.140	.646	1.000
	21	300	00	.346	.181	.403	.475	.282	.088	.229	.311	.409	.316	3.932	.790	1.300	1.161	.892
	22	300	25	.218	.174	.389	.323	.280	.135	.328	.339	.317	.295	1.615	.530	1.147	1.018	.949
	23	300	50	.247	.144	.373	.248	.421	.090	.328	.300	.146	.488	2.744	.439	1.243	1.699	.863
	24	300	75	.270	.146	.086	.338	.242	.102	.246	.136	.236	.242	2.647	.593	.632	1.432	1.000
	25	150	00	.160	.160	.191	.241	.243	.017	.152	.197	.190	.184	9.412	1.052	.969	1.268	1.321
	26	150	25	.150	.143	.132	.268	.178	.054	.044	.156	.160	.122	2.778	3.250	.846	1.675	1.459
	27	150	50	.123	.041	.063	.088	.140	.016	.061	.110	.061	.096	7.687	.672	.573	1.443	1.458
	28	150	75	.105	.039	.096	.129	.073	.012	.055	.083	.107	.092	8.750	.709	1.157	1.206	.794
	29	300	00	.148	.195	.298	.209	.250	.039	.139	.308	.138	.152	3.795	1.403	.968	1.514	1.644
	30	300	25	.085	.192	.206	.304	.199	.079	.192	.226	.262	.128	1.076	1.000	.911	1.160	1.555
	31	300	50	.048	.074	.074	.188	.231	.015	.139	.120	.142	.192	3.200	.532	.617	1.323	1.203
	32	300	75	.096	.048	.121	.165	.137	.088	.092	.116	.076	.137	1.091	.532	1.043	2.171	1.000

33	.048	.098	.093	.082	.131	.114	.036	.104	.076	.080	.122	.078	1.333	.942	1.223	1.025	1.073	1.461
34	.053	.081	.094	.112	.136	.144	.036	.110	.078	.112	.130	.142	1.472	.736	1.205	1.000	1.046	1.014
35	.074	.106	.139	.160	.174	.162	.054	.132	.114	.160	.170	.162	1.370	.803	1.219	1.000	1.023	1.000
36	.067	.191	.228	.262	.211	.231	.048	.218	.194	.262	.224	.220	1.395	.876	1.175	1.000	.941	1.050
37	.231	.329	.210	.255	.285	.309	.172	.360	.198	.256	.264	.296	1.343	.913	1.160	.996	1.079	1.043
38	.202	.255	.309	.246	.362	.316	.212	.274	.308	.238	.312	.302	.952	.930	1.003	1.033	1.160	1.046
39	.335	.534	.376	.280	.279	.322	.332	.566	.388	.282	.264	.364	1.009	.943	.969	.992	1.056	.884
40	.416	.478	.428	.489	.354	.328	.430	.512	.486	.426	.356	.358	.967	.933	.880	1.147	.994	.916
41	.099	.463	.496	.599	.592	.559	.080	.482	.466	.594	.592	.584	1.237	.960	1.064	1.008	1.000	.957
42	.110	.262	.361	.457	.581	.756	.096	.300	.344	.448	.542	.770	1.145	.873	1.049	1.020	1.071	.981
43	.093	.269	.275	.325	.342	.326	.086	.292	.260	.300	.348	.350	1.081	.921	1.057	1.083	.983	.931
44	.097	.245	.217	.278	.349	.389	.084	.248	.192	.264	.332	.424	1.154	.987	1.130	1.053	1.051	.917
45	.461	.511	.396	.369	.330	.255	.478	.596	.396	.380	.350	.296	.964	.857	1.000	.971	.942	.861
46	.461	.492	.275	.422	.600	.735	.480	.542	.280	.418	.618	.794	.960	.907	.982	1.009	.970	.925
47	.451	.556	.412	.440	.506	.491	.486	.610	.398	.444	.306	.292	.927	.911	1.035	.990	1.653	1.681
48	.369	.261	.236	.400	.388	.353	.396	.234	.238	.380	.398	.404	.931	1.115	.991	1.052	.974	.873
49	.141	.085	.096	.116	.366	.501	.128	.054	.090	.112	.318	.486	1.101	1.574	1.066	1.035	1.150	1.030
50	.169	.117	.126	.225	.322	.338	.148	.100	.102	.130	.310	.362	1.141	1.170	1.235	1.730	1.038	.933
51	.135	.097	.111	.151	.225	.250	.120	.086	.102	.160	.130	.268	1.125	1.127	1.088	.943	1.730	.932
52	.107	.088	.093	.135	.136	.218	.098	.074	.088	.142	.140	.232	1.091	1.189	1.056	.950	.971	.939
53	.215	.328	.262	.252	.265	.323	.218	.304	.292	.242	.328	.350	.986	1.078	.897	1.041	.807	.922
54	.164	.335	.232	.291	.184	.177	.164	.308	.324	.288	.232	.240	1.000	1.087	.716	1.010	.793	.737
55	.162	.275	.209	.315	.326	.275	.156	.278	.240	.324	.362	.332	1.038	.989	.870	.972	.900	.828
56	.207	.298	.224	.303	.320	.230	.200	.280	.242	.350	.314	.264	1.035	1.064	.925	.865	1.019	.871
57	.072	.076	.054	.127	.171	.259	.062	.090	.058	.130	.184	.264	1.161	.844	.931	.976	.929	.981
58	.056	.062	.042	.085	.096	.134	.048	.070	.044	.102	.108	.126	1.166	.885	.954	.833	.888	1.063
59	.069	.082	.087	.091	.119	.192	.060	.068	.084	.100	.126	.188	1.150	1.205	1.035	.910	.944	1.021
60	.066	.095	.064	.113	.156	.197	.052	.080	.064	.118	.160	.180	1.269	1.187	1.000	.957	.975	1.094
61	.173	.274	.262	.327	.308	.293	.196	.268	.262	.294	.334	.338	.882	1.022	1.000	1.112	.922	.866
62	.183	.268	.244	.286	.257	.239	.176	.242	.324	.268	.314	.276	1.039	1.107	.753	.910	.958	.865
63	.230	.270	.217	.275	.197	.078	.226	.240	.276	.242	.268	.110	1.017	1.125	.786	1.136	.735	.709
64	.248	.271	.225	.286	.185	.185	.232	.230	.240	.214	.192	.188	1.068	1.178	.937	1.336	.963	.984
13*	.402	.977	.707	.694	.718		.420	.934	.714	.704	.746		.957	1.046	.990	.985	.962	

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*Not included in computation of means

TABLE II (Continued)

#	GROSS PRODUCTIVITY IN mM CO_2/L/DAY					TOTAL RESPIRATION IN mM CO_2/L/DAY					P/R RATIO (GROSS)				
01	.206	.077	.119	.141	.178	.114	.094	.092	.124	.176	1.807	.819	1.293	1.137	1.011
02	.204	.125	.226	.224	.192	.068	.152	.190	.198	.188	3.000*	.822	1.189	1.131	1.021
03	.176	.096	.146	.176	.177	.108	.108	.116	.158	.154	1.630	.889	1.259	1.114	1.149
04	.360	.286	.389	.385	.269	.288	.300	.354	.318	.210	1.250	.953	1.099	1.211	1.281
05	.265	.174	.163	.281	.217	.252	.210	.172	.284	.254	1.052	.829	.948	.989	.854
06	.225	.189	.281	.322	.260	.248	.224	.238	.316	.286	.907	.844	1.181	1.019	.909
07	.200	.235	.286	.319	.300	.336	.266	.320	.344	.300	.595	.883	.894	.927	1.000
08	.329	.342	.463	.457	.343	.356	.342	.268	.394	.316	.924	1.000	1.728	1.160	1.085
09	.622	.628	.768	.667	.584	.348	.586	.818	.618	.394	1.787	1.072	.939	1.079	1.482
10	.598	.434	.502	.630	.435	.290	.418	.446	.448	.410	2.062*	1.038	1.126	1.406	1.061
11	.545	.358	.380	.555	.374	.252	.350	.388	.496	.440	2.163*	1.023	.979	1.119	.850
12	.545	.268	.270	.387	.438	.324	.266	.276	.342	.444	1.682	1.007	.978	1.132	.986
13	.681	.790	.904	1.096	.804	.420	.736	.868	.808	.824	1.621	1.073	1.041	1.359	.976
14	.672	.784	.360	.436	.531	.478	.788	.442	.464	.612	1.406	.995	.814	.940	.868
15	.630	.656	.458	.685	.477	.386	.740	.426	.514	.486	1.632	.886	1.075	1.333	.981
16	.613	.349	.591	.569	.452	.430	.480	.572	.494	.388	1.426	.727	1.033	1.152	1.165
17	.255	.396	.323	.395	.394	.042	.396	.334	.366	.416	6.071*	1.000	.967	1.079	.947
18	.350	.317	.346	.301	.313	.048	.306	.318	.288	.364	7.292*	1.036	1.088	1.045	.860
19	.323	.456	.406	.448	.449	.230	.574	.414	.448	.482	1.404	.794	.981	1.000	.932
20	.190	.224	.458	.418	.468	.030	.282	.428	.508	.468	6.333*	.794	1.070	.823	1.000
21	.434	.410	.714	.884	.598	.176	.458	.622	.818	.632	2.466*	.895	1.148	1.081	.946
22	.353	.502	.728	.640	.575	.270	.656	.678	.634	.590	1.307	.765	1.074	1.009	.975
23	.337	.472	.673	.394	.909	.180	.656	.600	.192	.976	1.872	.719	1.122	2.052	.931
24	.372	.392	.222	.574	.484	.204	.492	.272	.472	.484	1.824	.797	.816	1.216	1.000
25	.177	.312	.388	.431	.427	.034	.304	.394	.380	.368	5.205*	1.026	.985	1.134	1.160
26	.204	.187	.288	.428	.300	.108	.088	.312	.320	.244	1.889	2.125	.923	1.337	1.229
27	.139	.102	.173	.149	.236	.032	.122	.220	.122	.192	4.344*	.836	.786	1.221	1.229
28	.117	.094	.179	.236	.165	.024	.110	.166	.214	.184	4.875*	.855	1.078	1.103	.897
29	.187	.334	.606	.347	.402	.078	.278	.616	.276	.304	2.397*	1.201	.984	1.257	1.322
30	.164	.384	.432	.566	.327	.158	.384	.452	.524	.256	1.038	1.000	.956	1.080	1.277
31	.063	.213	.194	.330	.423	.030	.278	.240	.284	.384	2.133*	.766	.808	1.162	1.102
32	.184	.140	.237	.241	.274	.176	.184	.232	.152	.274	1.045	.761	1.022	1.586	1.000

	33	600	75	.030	.046	.055	.042	.070	.075	.018	.052	.038	.040	.061	.039	1.663	.895	1.448	1.050	1.147	1.901
	34	600	50	.035	.026	.055	.056	.071	.073	.018	.055	.039	.056	.065	.071	1.945	.446	1.415	1.000	1.093	1.043
	35	600	25	.047	.040	.082	.080	.089	.081	.027	.066	.057	.080	.085	.081	1.730	.614	1.434	1.000	1.046	1.000
	36	600	00	.043	.082	.131	.131	.099	.121	.024	.109	.097	.131	.112	.110	1.790	.753	1.354	1.000	.882	1.107
	37	075	75	.075	.149	.111	.127	.153	.161	.086	.180	.099	.128	.132	.148	.873	.826	1.119	.991	1.162	1.088
	38	075	50	.096	.118	.155	.127	.206	.165	.106	.137	.154	.119	.156	.151	.906	.857	1.004	1.069	1.322	1.097
TEMP. 23 C	39	075	25	.169	.251	.182	.139	.147	.140	.166	.283	.194	.141	.132	.182	1.021	.887	.936	.988	1.116	.768
	40	075	00	.201	.222	.185	.246	.176	.149	.215	.256	.243	.213	.178	.179	.935	.867	.761	1.153	.989	.832
	41	600	00	.059	.222	.263	.302	.296	.267	.040	.241	.233	.297	.296	.292	1.482	.920	1.129	1.017	1.000	.914
	42	600	25	.062	.112	.189	.233	.310	.371	.048	.150	.172	.224	.271	.385	1.289	.746	1.104	1.042	1.142	.964
	43	600	50	.050	.123	.145	.175	.168	.151	.043	.146	.130	.150	.174	.175	1.183	.845	1.111	1.168	.968	.862
	44	600	75	.055	.121	.121	.146	.183	.177	.042	.124	.096	.132	.166	.212	1.319	.976	1.259	1.100	1.101	.835
	45	075	00	.222	.213	.198	.179	.155	.107	.239	.298	.198	.190	.175	.148	.930	.717	1.000	.941	.885	.726
	46	075	25	.221	.221	.135	.213	.291	.338	.240	.271	.140	.209	.309	.397	.921	.815	.964	1.019	.942	.852
	47	075	50	.208	.251	.213	.218	.253	.245	.243	.305	.199	.222	.253	.246	.854	.822	1.071	.978	1.000	.996
	48	075	75	.171	.144	.117	.210	.189	.151	.198	.117	.119	.190	.199	.202	.868	1.228	.979	1.101	.947	.750
	49	600	00	.077	.058	.051	.060	.207	.258	.064	.027	.045	.056	.159	.243	1.208	2.159	1.110	1.073	1.302	1.060
	50	600	25	.095	.067	.075	.110	.167	.157	.074	.050	.051	.115	.155	.181	1.284	1.336	1.481	.958	1.080	.867
	51	600	50	.075	.054	.060	.071	.110	.116	.060	.043	.051	.080	.115	.134	1.261	1.262	1.177	.898	.956	.866
	52	600	75	.058	.051	.049	.064	.066	.102	.049	.037	.044	.071	.070	.116	1.189	1.378	1.118	.901	.944	.876
	53	075	00	.106	.176	.116	.131	.101	.148	.109	.152	.146	.121	.164	.175	.968	1.154	.797	1.087	.614	.847
	54	075	25	.082	.181	.070	.147	.068	.057	.082	.154	.162	.144	.116	.120	1.000	1.175	.429	1.020	.587	.477
	55	075	50	.084	.136	.089	.153	.145	.109	.078	.139	.120	.162	.181	.166	1.077	.979	.744	.944	.801	.656
TEMP. 11 C	56	075	75	.107	.158	.103	.128	.163	.098	.100	.140	.121	.175	.157	.132	1.068	1.135	.856	.729	1.038	.740
	57	600	00	.041	.031	.025	.062	.079	.127	.031	.045	.029	.065	.092	.132	1.321	.690	.869	.954	.862	.962
	58	600	25	.032	.027	.020	.034	.042	.071	.024	.035	.022	.051	.054	.063	1.333	.769	.913	.672	.777	1.123
	59	600	50	.039	.048	.045	.041	.056	.098	.030	.034	.042	.050	.063	.094	1.285	1.426	1.062	.819	.883	1.045
	60	600	75	.040	.045	.032	.054	.076	.107	.026	.040	.032	.059	.080	.090	1.563	1.119	1.000	.912	.951	1.197
	61	075	00	.075	.140	.131	.180	.139	.126	.098	.134	.131	.147	.169	.167	.758	1.045	1.000	1.224	.822	.752
	62	075	25	.095	.147	.082	.152	.100	.101	.088	.121	.162	.134	.157	.138	1.077	1.217	.507	1.136	.637	.733
	63	075	50	.117	.150	.079	.154	.063	.023	.113	.120	.138	.121	.134	.055	1.031	1.248	.574	1.274	.466	.410
	64	075	75	.132	.156	.105	.179	.089	.091	.116	.115	.120	.107	.096	.094	1.137	1.356	.875	1.685	.929	.964
	13'	300	00	.192	.510	.350	.342	.345		.210	.467	.357	.352	.373		.913	1.092	.981	.971	.926	

TDIS = Total dissolved inorganic solids in ppm
T = Turbidity in ppm

TABLE II (Continued)

#	BIOMASS IN G/L					GROSS PRODUCTIVITY PER UNIT BIOMASS IN MG/G				
01	.120	.130	.210	.242	.180	1.717	.592	.567	.583	.989
02	.146	.146	.146	.166	.180	1.397	.856	1.548	1.349	1.067
03	.092	.142	.140	.154	.170	1.913	.676	1.043	1.143	1.041
04	.134	.144	.304	.166	.200	2.686	1.986	1.280	2.319	1.345
05	.270	.330	.276	.258	.298	.981	.527	.591	1.089	.728
06	.282	.244	.250	.298	.338	.798	.775	1.124	1.081	.769
07	.236	.272	.390	.252	.328	.847	.864	.733	1.266	.915
08	.258	.238	.286	.282	.382	1.275	1.437	1.619	1.621	.898
09	.154	.176	.272	.262	.286	4.039	3.568	2.824	2.546	2.042
10	.146	.184	.310	.200	.358	4.096	2.359	1.619	3.150	1.215
11	.248	.154	.300	.250	.276	2.198	2.325	1.267	2.220	1.355
12	.174	.198	.124	.120	.282	3.132	1.354	2.177	3.225	1.553
13	.330	.324	.500	.420	.458	2.064	2.438	1.808	2.609	1.755
14		.262	.534	.376	.668		2.992	.674	1.160	.795
15	.234	.280	.352	.368	.814	2.692	2.343	1.301	1.861	.586
16	.250	.304	.370	.330	.360	2.452	1.148	1.597	1.724	1.255
17	.164	.166	.342	.256	.262	1.555	2.385	.944	1.543	1.504
18	.222	.150	.250	.256	.342	1.577	2.113	1.384	1.176	.915
19	.142	.158	.252	.222	.232	2.275	2.886	1.611	2.018	1.935
20	.160	.152	.228	.242	.214	1.187	1.474	2.009	1.727	2.187
21	.274	.244	.374	.296	.360	1.584	1.680	1.909	2.986	1.661
22	.242	.252	.362	.288	.372	1.459	1.992	2.011	2.222	1.546
23		.262	.344	.282	.364	1.338	1.801	1.956	1.397	2.497
24	.278	.254	.360	.232	.336	1.543	1.543	.617	2.474	1.440
25	.112	.132	.250	.200	.196	1.580	2.364	1.552	2.155	2.178
26	.094	.128	.246	.172	.208	2.170	1.461	1.171	2.488	1.442
27	.138		.248	.154	.176	1.007		.698	.967	1.341
28	.146	.138		.154	.192	.801	.681		1.532	.859
29	.250	.232	.330	.282	.296	.748	1.440	1.836	1.230	1.358
30	.236	.242	.324	.330	.292	.695	1.587	1.333	1.715	1.120
31	.324	.246	.308	.176	.274	.194	.866	.630	1.875	1.544
32	.236	.236	.330	.174	.264	.780	.593	.718	1.385	1.038

33	.520	.486	.440	.550	.550	.514	0.092	0.201	0.211	0.149	0.238	0.221
34		.492	.492	.556	.520	.568		0.164	0.191	0.201	0.261	0.253
35	.580	.612	.516	.518	.462	.532	0.127	0.173	0.269	0.308	0.376	0.304
36	.552	.568	.506	.564	.536	.560	0.121	0.336	0.450	0.464	0.393	0.412
37	.058	.086	.126	.128	.110	.116	3.982	3.825	1.666	1.992	2.590	2.663
38	.078	.096	.170	.122	.122	.180	2.589	2.656	1.817	2.016	2.967	1.755
39	.180	.100	.166	.182	.194	.220	1.861	5.340	2.265	1.538	1.438	1.463
40	.066	.060	.136	.174	.126	.172	6.303	7.966	3.147	2.810	2.809	1.906
41	.498	.624	.456	.714	.670	.596	0.198	0.741	1.087	0.838	0.883	0.937
42	.516	.598	.386	.592	.522	.586	0.213	0.438	0.935	0.771	1.113	1.290
43	.484	.516	.532	.652	.550	.510	0.192	0.521	0.516	0.498	0.621	0.639
44	.620	.550	.492	.660	.512	.612	0.156	0.445	0.441	0.421	0.681	0.635
45	.056	.112	.200	.208	.236	.208	8.232	4.562	1.980	1.774	1.398	1.225
46	.090	.192	.208	.286	.286	.312	5.122	2.562	1.322	1.475	2.097	3.533
47	.080	.132	.142	.188	.160	.222	5.637	4.212	2.901	2.340	4.773	2.211
48	.080	.102	.158	.198	.186	.338	4.612	2.558	1.493	2.020	2.086	1.044
49	.555	.514	.430	.502	.452	.516	0.254	0.165	0.223	0.231	0.809	0.970
50	.560	.530	.512	.594	.462	.502	0.301	0.220	0.246	0.378	0.696	0.673
51	.535	.594	.486	.532	.438	.490	0.252	0.163	0.228	0.283	0.513	0.510
52	.630	.290	.508	.622	.548	.494	0.169	0.303	0.183	0.217	0.248	0.441
53	.070	.140	.126	.132	.146	.144	3.071	2.342	2.079	1.909	1.815	2.243
54	.082	.080	.090	.126	.104	.152	2.000	4.187	2.577	2.309	1.769	1.164
55	.082	.076	.132	.136	.136	.238	1.975	3.618	1.583	2.316	2.397	1.155
56		.084	.118	.142	.132	.178		3.547	1.898	2.133	2.424	1.292
57		.534	.450	.536	.544	.492		0.142	0.120	0.236	0.314	0.526
58		.616	.482	.562	.504	.592		0.100	0.087	0.151	0.190	0.226
59		.610	.402	.538	.560	.468		0.134	0.216	0.169	0.212	0.410
60		.566	.418	.534	.532	.470		0.167	0.153	0.211	0.293	0.419
61		.130	.114	.206	.120	.156		2.107	2.298	1.587	2.566	1.878
62		.150	.108	.122	.114	.142		1.786	2.259	2.344	2.254	1.683
63		.088	.066	.216	.118	.118		3.068	3.287	1.273	1.669	0.661
64		.110	.074	.122	.124	.118		2.463	3.040	2.344	1.491	1.567
13'		.394		.462	.392	.512		2.479		1.502	1.831	

APPENDIX B

TABLE

FACTORIAL ANALYSIS, COE
EFFECTS AND R

Factor Levels A B C D	0 0 0 0	0 0 0 1	0 0 1 0	0 0 1 1	0 1 0 0	0 1 0 1	0 1 1 0	0 1 1 1	0 2 0 0	0 2 0 1	0 2 1 0	0 2 1 1	0 3 0 0	0 3 0 1	0 3 1 0	0 3 1 1	1 0 0 0	1 0 0 1	1 0 1 0	1 0 1 1	1 1 0 0	1 1 0 1	1 1 1 0	1 1 1 1	1 2 0 0	1 2 0 1	1 2 1 0	1 2 1 1	1 3 0 0	1 3 0 1	1 3 1 0	1 3 1 1	2 0 0 0	2 0 0 1	2 0 1 0	2 0 1 1
Mean Prod.	.272	.415	.274	.387	.389	.338	.377	.654	.422	.387	.652	.855	.126	.198	.217	.468	.246	.354	.230	.497	.281	.154	.319	.500	.375	.268	.560	.556	.079	.135	.216	.420	.211	.281	.260	.476
D	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
C	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+
A_L	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+
A_Q	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B_L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3	3	3	3	3	-	-	+	+	+	+	3	3	3	3	-3	-3	-3	-3
B_Q	-3	-3	-3	-3	-	-	-	-	+	+	+	+	3	3	3	3	-3	-3	-3	-3	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+
A_C	+	+	+	+	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	-	-	3	3	3	3	3	3	3	3	3	3	-3	-3	-3	-3
B_C	-	-	-	-	3	3	3	3	-3	-3	-3	-3	+	+	+	+	-	-	-	-	3	3	3	3	-3	-3	-3	-3	+	+	+	+	-	-	-	-
A_CB_C	+	+	+	+	-3	-3	-3	-3	3	3	3	3	-	-	-	-	-3	-3	-3	-3	9	9	9	9	-9	-9	-9	-9	3	3	3	3	3	3	3	3
CD	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+
A_LD	+3	-3	+3	-3	3	-3	3	-3	3	-3	3	-3	3	-3	3	-3	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	-	+	-	+
A_QD	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
A_CD	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	-3	3	-3	3	-3	3	-3	3	-3	3	-3	3	-3	3	-3	3	3	-3	3	-3
B_LD	3	-3	3	-3	+	-	+	-	-	+	-	+	-3	3	-3	3	3	-3	3	-3	+	-	+	-	-	+	-	+	-3	3	-3	3	3	-3	3	-3
B_QD	-	+	-	+	+	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	+	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+
B_CD	+	-	+	-	-3	3	-3	3	3	-3	3	-3	-	+	-	+	+	-	+	-	-3	3	-3	3	3	-3	3	-3	-	+	-	+	+	-	+	-
A_LC	3	3	-3	-3	3	3	-3	-3	3	3	-3	-3	3	3	-3	-3	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	-	-	+	+
A_QC	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-
A_CC	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	-3	-3	3	3	-3	-3	3	3	-3	-3	3	3	-3	-3	3	3	3	3	-3	-3
B_LC	3	3	-3	-3	+	+	-	-	-	-	+	+	-3	-3	3	3	3	3	-3	-3	+	+	-	-	-	-	+	+	-3	-3	3	3	3	3	-3	-3
B_QC	-	-	+	+	+	+	-	-	+	+	-	-	-	-	+	+	-	-	+	+	+	+	-	-	+	+	-	-	-	-	+	+	-	-	+	+
B_CC	+	+	-	-	-3	-3	3	3	3	3	-3	-3	-	-	+	+	+	+	-	-	-3	-3	3	3	3	3	-3	-3	-	-	+	+	+	+	-	-
A_LB_L	9	9	9	9	3	3	3	3	-3	-3	-3	-3	-9	-9	-9	-9	3	3	3	3	+	+	+	+	-	-	-	-	-3	-3	-3	-3	-3	-3	-3	-3
A_LB_Q	-3	-3	-3	-3	3	3	3	3	3	3	3	3	-3	-3	-3	-3	-	-	-	-	+	+	+	+	+	+	+	+	-	-	-	-	+	+	+	+
A_LB_C	3	3	3	3	-9	-9	-9	-9	9	9	9	9	-3	-3	-3	-3	+	+	+	+	-3	-3	-3	-3	3	3	3	3	-	-	-	-	-	-	-	-
A_QB_L	-3	-3	-3	-3	-	-	-	-	+	+	+	+	3	3	3	3	3	3	3	3	+	+	+	+	-	-	-	-	-3	-3	-3	-3	3	3	3	3
A_QB_Q	+	+	+	+	-	-	-	-	-	-	-	-	+	+	+	+	-	-	-	-	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-
A_QB_C	-	-	-	-	3	3	3	3	-3	-3	-3	-3	+	+	+	+	+	+	+	+	-3	-3	-3	-3	3	3	3	3	-	-	-	-	+	+	+	+
A_CB_L	3	3	3	3	+	+	+	+	-	-	-	-	-3	-3	-3	-3	-9	-9	-9	-9	-3	-3	-3	-3	3	3	3	3	9	9	9	9	9	9	9	9
A_CB_Q	-	-	-	-	+	+	+	+	+	+	+	+	-	-	-	-	3	3	3	3	-3	-3	-3	-3	-3	-3	-3	-3	3	3	3	3	-3	-3	-3	-3
A_LB_LC	-9	-9	+9	+9	-3	-3	3	3	3	3	-3	-3	9	9	-9	-9	-3	-3	3	3	-	-	+	+	+	+	-	-	3	3	-3	-3	3	3	-3	-3
A_LB_QC	3	3	-3	-3	-3	-3	3	3	-3	-3	3	3	3	3	-3	-3	+	+	-	-	-	-	+	+	-	-	+	+	+	+	-	-	-	-	+	+
A_LB_CC	-3	-3	3	3	9	9	-9	-9	-9	-9	9	9	3	3	-3	-3	-	-	+	+			-3	-3	-3	-3	3	3	+	+	-	-	+	+	-	-
A_QB_LC	3	3	-3	-3	+	+	-	-	-	-	+	+	-3	-3	3	3	-3	-3	3	3	-	-	+	+	+	+	-	-	3	3	-3	-3	-3	-3	3	3
A_QB_QC	-	-	+	+	+	+	-	-	+	+	-	-	-	-	+	+	+	+	-	-	-	-	+	+	-	-	+	+	+	+	-	-	+	+	-	-
A_QB_CC	+	+	-	-	-3	-3	3	3	3	3	-3	-3	-	-	+	+	-	-	+	+	3	3	-3	-3	-3	-3	3	3	+	+	-	-	-	-	+	+
A_CB_LC	-3	-3	3	3	-	-	+	+	+	+	-	-	3	3	-3	-3	9	9	-9	-9	3	3	-3	-3	-3	-3	3	3	-9	-9	9	9	-9	-9	9	9
A_CB_QC	+	+	-	-	-	-	+	+	-	-	+	+	+	+	-	-	-3	-3	3	3	3	3	-3	-3	3	3	-3	-3	-3	-3	3	3	3	3	-3	-3
A_CB_CC	-	-	+	+	3	3	-3	-3	-3	-3	3	3	+	+	-	-	3	3	-3	-3	-9	-9	9	9	9	9	-9	-9	-3	-3	3	3	-3	-3	3	3
A_LB_LD	-9	9	-9	9	-3	3	-3	3	3	-3	3	-3	9	-9	9	-9	-3	3	-3	3	-	+	-	+	+	-	+	-	3	-3	3	-3	3	-3	3	-3
A_LB_QD	3	-3	3	-3	-3	3	-3	3	-3	3	-3	3	3	-3	3	-3	+	-	+	-	-	+	-	+	-	+	-	+	+	-	+	-	-	+	-	+
A_LB_CD	-3	3	-3	3	9	-9	9	-9	-9	9	-9	9	3	-3	3	-3	-	+	-	+	3	-3	3	-3	-3	3	-3	3	+	-	+	-	+	-	+	-
A_QB_LD	3	-3	3	-3	+	-	+	-	-	+	-	+	-3	3	-3	3	-3	3	-3	3	-	+	-	+	+	-	+	-	3	-3	3	-3	-3	3	-3	3
A_QB_QD	-	+	-	+	+	-	+	-	+	-	+	-	-	+	-	+	+	-	+	-	-	+	-	+	-	+	-	+	+	-	+	-	+	-	+	-
A_QB_CD	+	-	+	-	-3	3	-3	3	3	-3	3	-3	-	+	-	+	-	+	-	+	3	-3	3	-3	-3	3	-3	3	+	-		-	-	+	-	+
A_CB_LD	-3	3	-3	3	-	+	-	+	+	-	+	-	3	-3	3	-3	9	-9	9	-9	3	-3	3	-3	-3	3	-3	3	-9	9	-9	9	-9	9	-9	9
A_CB_QD	+	-	+	-	-	+	-	+	-	+	-	+	+	-	+	-	-3	3	-3	3	3	-3	3	-3	3	-3	3	-3	-3	3	-3	3	3	-3	3	-3
A_CB_CD	-	+	-	+	3	-3	3	-3	-3	3	-3	3	+	-	+	-	3	-3	3	-3	-9	9	-9	9	9	-9	9	-9	-3	3	-3	3	-3	3	-3	3
A_LB_LCD	9	-9	-9	9	3	-3	-3	3	-3	3	3	-3	-9	9	9	-9	3	-3	-3	3	+	-	-	+	-	+	+	-	-3	3	3	-3	-3	3	3	-3
A_LB_QCD	-3	3	3	-3	3	-3	-3	3	3	-3	-3	3	-3	3	3	-3	-	+	+	-	+	-	-	+	+	-	-	+	-	+	+	-	+	-	-	+
A_LB_CCD	3	-3	-3	3	-9	9	9	-9	9	-9	-9	9	-3	3	3	-3	+	-	-	+	-3	3	3	-3	3	-3	-3	3	-	+	+	-	-	+	+	-
A_QB_LCD	-3	3	3	-3	-	+	+	-	+	-	-	+	3	-3	-3	3	3	-3	-3	3	+	-	-	+	-	+	+	-	-3	3	3	-3	3	-3	-3	3
A_QB_QCD	+	-	-	+	-	+	+	-	-	+	+	-	+	-	-	+	-	+	+	-	+	-	-	+	+	-	-	+	-	+	+	-	-	+	+	-
A_QB_CCD	-	+	+	-	3	-3	-3	3	-3	3	3	-3	+	-	-	+	+	-	-	+	-3	3	3	-3	3	-3	-3	3	-	+	+	-	+	-	-	+
A_CB_LCD	3	-3	-3	3	+	-	-	+	-	+	+	-	-3	3	3	-3	-9	9	9	-9	-3	3	3	-3	3	-3	-3	3	9	-9	-9	9	9	-9	-9	9
A_CB_QCD	-	+	+	-	+	-	-	+	+	-	-	+	-	+	+	-	3	-3	-3	3	-3	3	3	-3	-3	3	3	-3	3	-3	-3	3	-3	3	3	-3
A_CB_CCD	+	-	-	+	-3	3	3	-3	3	-3	-3	3	-	+	+	-	-3	3	3	-3	9	-9	-9	9	-9	9	9	-9	3	-3	-3	3	3	-3	-3	3
A_LCD	-3	3	3	-3	-3	3	3	-3	-3	3	3	-3	-3	3	3	-3	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	+	-	-	+
A_QCD	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-
A_CCD	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	3	-3	-3	3	3	-3	-3	3	3	-3	-3	3	3	-3	-3	3	-3	3	3	-3
B_LCD	-3	3	3	-3	-	+	+	-	-	+	+	-	3	-3	-3	3	-3	3	3	-3	-	+	+	-	+	-	-	+	3	-3	-3	3	-3	3	3	-3
B_QCD	+	-	-	+	-	+	+	-	-	+	+	-	+	-	-	+	+	-	-	+	-	+	+	-	-	+	+	-	+	-	-	+	+	-	-	+
B_CCD	-	+	+	-	3	-3	-3	3	-3	3	3	-3	+	-	-	+	-	+	+	-	3	-3	-3	3	-3	3	3	-3	+	-	-	+	-	+	+	-

Factor A = Turbidity, B = TDIS, C = Light Intensity, D = Temperature.
Subscript L = Linear Effect, Q = Quadratic Effect, C = Cubic Effect.
Level 0 is lowest, 3 is highest.

I

FFICIENTS FOR CONTRASTS,
ANK OF EFFECTS

2100	2101	2110	2111	2200	2201	2210	2211	2300	2301	2310	2311	3000	3001	3010	3011	3100	3101	3110	3111	3200	3201	3210	3211	3300	3301	3310	3311					
.165	.192	.416	.417	.290	.255	.557	.581	.106	.103	.161	.271	.233	.269	.263	.334	.168	.144	.392	.382	.215	.220	.409	.515	.115	.094	.129	.262	Q	K	$\sqrt{K}$	Effect	Rank
-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	2.257	64	8.0	.2821	4
-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	5.507	64	8.0	.6884	1
+	+	+	+	+	+	+	+	+	+	+	+	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	-7.309	320	17.9	.4085	3
-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0.64'	64	8.0	.0804	18
-	-	-	-	+	+	+	+	3	3	3	3	-3	-3	-3	-3	-	-	-	-	+	+	+	+	3	3	3	3	0.786	320	17.9	.2167	7
-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	+	+	+	+	-4.303	64	8.0	.5379	2
-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-0.943	320	17.9	.0527	30
3	3	3	3	-3	-3	-3	-3	+	+	+	+	-	-	-	-	3	3	3	3	-3	-3	-3	-3	+	+	+	+	-7.389	320	17.9	.4130	*
-9	-9	-9	-9	9	9	9	9	-3	-3	-3	-3	-	-	-	-	3	3	3	3	-3	-3	-3	-3	+	+	+	+	0.917	1600	40.0	.0229	49
+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	2.029	64	8.0	.2536	6
-	+	-	+	-	+	-	+	-	+	-	+	-3	3	-3	3	-3	3	-3	3	-3	3	-3	3	-3	3	-3	3	-2.199	320	17.9	.1229	12
+	-	+	-	+	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	0.281	64	8.0	.0351	44
3	-3	3	-3	3	-3	3	-3	3	-3	3	-3	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-0.173	320	17.9	.0097	55
+	-	+	-	-	+	-	+	-3	3	-3	3	3	-3	3	-3	+	-	+	-	-	+	-	+	-3	3	-3	3	-0.783	320	17.9	.0438	39
+	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	+	-	+	-	+	-	+	-	-	+	-	+	1.395	64	8.0	.1744	8
-3	3	-3	3	3	-3	3	-3	-	+	-	+	+	-	+	-	-3	3	-3	3	3	-3	3	-3	-	+	-	+	0.129	320	17.9	.0072	56
-	-	+	+	-	-	+	+	-	-	+	+	-3	-3	3	3	-3	-3	3	3	-3	-3	3	3	-3	-3	3	3	-0.197	320	17.9	.0110	54
+	+	-	-	+	+	-	-	+	+	-	-	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-0.377	64	8.0	.0471	35
3	3	-3	-3	3	3	-3	-3	3	3	-3	-3	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+	-0.499	320	17.9	.0279	45
+	+	-	-	-	-	+	+	-3	-3	3	3	3	3	-3	-3	+	+	-	-	-	-	+	+	-3	-3	3	3	2.871	320	17.9	.1605	9
+	+	-	-	+	+	-	-	-	-	+	+	-	-	+	+	+	+	-	-	+	+	-	-	-	-	+	+	-2.251	64	8.0	.2814	5
-3	-3	3	3	3	3	-3	-3	-	-	+	+	+	+	-	-	-3	-3	3	3	3	3	-3	-3	-	-	+	+	-1.133	320	17.9	.0633	25
-	-	-	-	+	+	+	+	3	3	3	3	-9	-9	-9	-9	-3	-3	-3	-3	3	3	3	3	9	9	9	9	-2.637	1600	40.0	.0659	23
-	-	-	-	-	-	-	-	+	+	+	+	3	3	3	3	-3	-3	-3	-3	-3	-3	-3	-3	3	3	3	3	2.745	320	17.9	.1534	10
3	3	3	3	-3	-3	-3	-3	+	+	+	+	-3	-3	-3	-3	9	9	9	9	-9	-9	-9	-9	3	3	3	3	2.011	1600	40.0	.0503	32
+	+	+	+	-	-	-	-	-3	-3	-3	-3	-3	-3	-3	-3	-	-	-	-	+	+	+	+	3	3	3	3	0.511	320	17.9	.0286	45
+	+	+	+	+	+	+	+	-	-	-	-	+	+	+	+	-	-	-	-	-	-	-	-	+	+	+	+	-0.623	64	8.0	.0779	19
-3	-3	-3	-3	3	3	3	3	-	-	-	-	-	-	-	-	3	3	3	3	-3	-3	-3	-3	+	+	+	+	1.167	320	17.9	.0652	24
3	3	3	3	-3	-3	-3	-3	-9	-9	-9	-9	-3	-3	-3	-3	-	-	-	-	+	+	+	+	3	3	3	3	0.261	1600	40.0	.0065	57
3	3	3	3	3	3	3	3	-3	-3	-3	-3	+	+	+	+	-	-	-	-	-	-	-	-	+	+	+	+	1.475	320	17.9	.0824	17
+	+	-	-	-	-	+	+	-3	-3	3	3	9	9	-9	-9	3	3	-3	-3	-3	-3	3	3	-9	-9	9	9	-4.721	1600	40.0	.1180	13
+	+	-	-	+	+	-	-	-	-	+	+	-3	-3	3	3	3	3	-3	-3	3	3	-3	-3	-3	-3	3	3	-0.315	320	17.9	.0176	52
-3	-3	3	3	3	3	-3	-3	-	-	+	+	3	3	-3	-3	-9	-9	9	9	9	9	-9	-9	-3	-3	3	3	5.015	1600	40.0	.1254	11
-	-	+	+	+	+	-	-	3	3	-3	-3	3	3	-3	-3	+	+	-	-	-	-	+	+	-3	-3	3	3	0.815	320	17.9	.0456	37
-	-	+	+	-	-	+	+	+	+	-	-	-	-	+	+	+	+	-	-	+	+	-	-	-	-	+	+	-0.431	64	8.0	.0539	28
3	3	-3	-3	-3	-3	3	3	+	+	-	-	+	+	-	-	-3	-3	3	3	3	3	-3	-3	-	-	+	+	-0.445	320	17.9	.0249	48
-3	-3	3	3	3	3	-3	-3	9	9	-9	-9	3	3	-3	-3	+	+	-	-	-	-	+	+	-3	-3	3	3	1.493	1600	40.0	.0373	42
-3	-3	3	3	-3	-3	3	3	3	3	-3	-3	-	-	+	+	+	+	-	-	+	+	-	-	-	-	+	+	0.875	320	17.9	.0489	33
9	9	-9	-9	-9	-9	9	9	3	3	-3	-3	+	+	-	-	-3	-3	3	3	3	3	-3	-3	-	-	+	+	-1.653	1600	40.0	.0413	40
+	-	+	-	-	+	-	+	-3	3	-3	3	9	-9	9	-9	3	-3	3	-3	-3	3	-3	3	-9	9	-9	9	-0.042	1600	40.0	.0010	62
+	-	+	-	+	-	+	-	-	+	-	+	-3	3	-3	3	3	-3	3	-3	3	-3	3	-3	-3	3	-3	3	-0.339	320	17.9	.0189	51
-3	3	-3	3	3	-3	3	-3	-	+	-	+	3	-3	3	-3	-9	9	-9	9	9	-9	9	-9	-3	3	-3	3	-2.461	1600	40.0	.0615	26
-	+	-	+	+	-	+	-	3	-3	3	-3	3	-3	3	-3	+	-	+	-	-	+	-	+	-3	3	-3	3	1.281	320	17.9	.0716	20
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3	-3	3	-3	-3	3	-3	3	+	-	+	-	+	-	+	-	-3	3	-3	3	3	-3	3	-3	-	+	-	+	-0.507	320	17.9	.0283	46
-3	3	-3	3	3	-3	3	-3	9	-9	9	-9	3	-3	3	-3	+	-	+	-	-	+	-	+	-3	3	-3	3	1.841	1600	40.0	.0460	36
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9	-9	9	-9	-9	9	-9	9	3	-3	3	-3	+	-	+	-	-3	3	-3	3	3	-3	3	-3	-	+	-	+	0.655	1600	40.0	.0164	53
-	+	+	-	+	-	-	+	3	-3	-3	3	-9	9	9	-9	-3	3	3	-3	3	-3	-3	3	9	-9	-9	9	-0.055	1600	40.0	.0014	59
-	+	+	-	-	+	+	-	+	-	-	+	3	-3	-3	3	-3	3	3	-3	-3	3	3	-3	3	-3	-3	3	1.803	320	17.9	.1008	14
3	-3	-3	3	-3	3	3	-3	+	-	-	+	-3	3	3	-3	9	-9	-9	9	-9	9	9	-9	3	-3	-3	3	-2.755	1600	40.0	.0689	21
+	-	-	+	-	+	+	-	-3	3	3	-3	-3	3	3	-3	-	+	+	-	+	-	-	+	3	-3	-3	3	1.233	320	17.9	.0689	22
+	-	-	+	+	-	-	+	-	+	+	-	+	-	-	+	-	+	+	-	-	+	+	-	+	-	-	+	-0.465	64	8.0	.0581	27
-3	3	3	-3	3	-3	-3	3	-	+	+	-	-	+	+	-	3	-3	-3	3	-3	3	3	-3	+	-	-	+	0.021	320	17.9	.0011	60
3	-3	-3	3	-3	3	3	-3	-9	9	9	-9	-3	3	3	-3	-	+	+	-	+	-	-	+	3	-3	-3	3	-0.765	1600	40.0	.0191	50
3	-3	-3	3	3	-3	-3	3	-3	3	3	-3	+	-	-	+	-	+	+	-	-	+	+	-	+	-	-	+	-0.499	320	17.9	.0279	46
-9	9	9	-9	9	9	-9	9	-3	3	3	-3	-	+	+	-	3	-3	-3	3	-3	3	3	-3	+	-	-	+	2.055	1600	40.0	.0514	30
+	-	-	+	+	-	-	+	+	-	-	+	3	-3	-3	3	3	-3	-3	3	3	-3	-3	3	3	-3	-3	3	-1.659	320	17.9	.0927	15
-	+	+	-	-	+	+	-	-	+	+	-	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	0.009	64	8.0	.0011	61
-3	3	3	-3	-3	3	3	-3	-3	3	3	-3	+	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	0.867	320	17.9	.0485	34
-	+	+	-	+	-	-	+	3	-3	-3	3	-3	3	3	-3	-	+	+	-	-	+	+	-	3	-3	-3	3	0.051	320	17.9	.0029	58
-	+	+	-	-	+	+	-	+	-	-	+	+	-	-	+	-	+	+	-	-	+	+	-	+	-	-	+	-0.221	64	8.0	.0276	47
3	-3	-3	3	-3	3	3	-3	+	-	-	+	-	+	+	-	3	-3	-3	3	-3	3	3	-3	+	-	-	+	0.653	320	17.9	.0365	43

* Not Ranked; Blocked on this Contrast

VITA

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Candidate for the Degree of

Doctor of Philosophy

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