

LAND-WATER INTERACTIONS: EFFECTS OF INTRODUCED NUTRIENTS AND SOIL  
PARTICLES ON RESERVOIR PRODUCTIVITY

BY

Bruce L. Kimmel, Ph.D.  
Biological Station  
and  
Department of Zoology  
The University of Oklahoma  
Norman, Oklahoma 73019

OKLAHOMA WATER RESOURCES RESEARCH INSTITUTE  
OKLAHOMA STATE UNIVERSITY  
Stillwater, Oklahoma 74074

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## ABSTRACT

### LAND-WATER INTERACTIONS: EFFECTS OF INTRODUCED NUTRIENTS AND SOIL PARTICLES ON RESERVOIR PRODUCTIVITY

Land-to-water fluxes of nutrients and suspended particles are important determinants of water quality and trophic structure in reservoir ecosystems. An improved understanding of watershed runoff effects on reservoir productivity and water quality is particularly important for the U.S. Great Plains region where (1) man-made impoundments are primary resources for surface water supply and water-based recreation, and (2) non-point source inputs constitute the major contributions to reservoir nutrient loading. In this research, laboratory and field approaches were combined to investigate the effects of introduced nutrients and suspended soil particles on organic matter production in man-made impoundments.

Watershed runoff experiments and in situ monitoring of inflow events in Lake Texoma (Oklahoma-Texas) showed that turbidity associated with river-borne suspended particles reduced the thickness of the euphotic layer, and thereby resulted in light-limited phytoplankton photosynthesis within a larger portion of the water column. Nutrient desorption from suspended silt and clay particles enhanced nutrient availability for phytoplankton and bacterioplankton production, and was dependent on soil nutrient composition. Increased nutrient availability associated with watershed inflow stimulated phytoplankton production within the euphotic portion of the water column and, in combination with reduced algal photo-inhibition in near-surface layers, resulted in increased integral produc-

tion.

The presence of suspended particles did not have a major stimulatory effect on microheterotrophy, but resulted in a shift toward larger particles in the size distributions of both autotrophic and microheterotrophic activities. Highly turbid watershed runoff resulted in the vertical displacement of phytoplankton cells in both experimental water columns and during runoff events in Lake Texoma. These results suggest that ultraphytoplankton and free-living bacteria are coflocculated in the presence of high concentrations of suspended silt and clay particles.

In both simulated watershed runoff experiments and in situ monitoring of inflow events, the phytoplankton-bacterioplankton response to turbid inflow occurred in three distinct phases: (1) light limitation of photosynthetic activity, (2) partial removal of phytoplankton and bacterial cells from the water column by a combination of advective and vertical displacement, and (3) nutrient stimulation of photosynthetic activity and the physiological status of phytoplankton remaining in the euphotic portion of the water column. An analogous sequence and similar effects on planktonic communities should be expected to occur in different portions of lakes, reservoirs and estuaries possessing marked longitudinal gradients in silt-clay turbidity, nutrient availability and productivity.

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PARTICLES ON RESERVOIR PRODUCTIVITY

1. INTRODUCTION

Land-water interactions are important determinants of water quality and biological productivity in lacustrine ecosystems. The impact of nutrient loading on lake productivity and trophic status has been well studied; however, the ecological effects of suspended erosion products introduced along with inorganic nutrients via watershed runoff are less well recognized.

Because dams form barriers to natural drainage systems, most man-made impoundments receive large amounts of inorganic nutrients, erosion products (e.g., silt and clay particles), and particulate and dissolved organic materials from their watersheds. Such inputs, in addition to agricultural chemicals, urban stormwater runoff, municipal and industrial effluents, and a variety of particle-associated contaminants, exert increasing water quality impacts as reservoir watersheds become more intensively urbanized and agriculturally developed. Accelerated use of existing man-made impoundments for municipal and industrial water supply, power plant cooling systems, hydroelectric power generation, irrigation and recreation must also be expected in the near future. Most reservoir watershed inputs originate from non-point sources, and therefore, it is not usually feasible to control nutrient and sediment loading to reservoirs. Thus, a thorough understanding of watershed-reservoir interactions becomes necessary for predicting the water quality and ecological consequences of altering land-use patterns, agricultural practices, or the extent of urban and/or agricultural development

within reservoir watersheds.

Nutrient availability often exerts primary control over the photosynthetic production of organic matter in natural lakes (e.g., Edmondson 1961, 1970, 1972; Goldman 1968, 1972; Schindler et al. 1971, Schindler 1975), and empirical models based on annual nutrient loading rates provide reasonable predictions of algal biomass and lake trophic state (e.g., Vollenweider 1968, Dillon and Rigler 1974, Oglesby and Schaffner 1978). However, in relatively nutrient-rich but turbid reservoirs, light availability may become the more important limiting factor and serve to moderate the influence of nutrient loading on algal production. For this and other reasons, a number of investigators have questioned the adequacy of nutrient loading models for application to reservoirs (e.g., Jones and Bachmann 1975, 1976, Lind 1979, Placke and Poppe 1980).

An improved knowledge of watershed runoff effects on reservoir productivity and water quality is particularly necessary in the U.S. Great Plains region, where (i) man-made impoundments are important resources for surface water supply and water-based recreation, and (ii) non-point source inputs via watershed runoff constitute the major contributions to reservoir nutrient loading. Great Plains reservoirs have much higher watershed area: lake surface area ratios than do natural lakes in the same region (Marzolf 1980), and most receive drainage from fertile watersheds having a high percentage of erodable clay soils. High turbidity caused by suspended silt and clay particles has long been recognized as a major factor limiting the biological productivity of midwestern and southwestern impoundments (e.g., Ellis 1936, Moore 1937, Harris and Silvey 1940, Claffey 1955, Wallen 1951, 1955, Buck 1956, Irwin and Stevenson 1951, Jackson and Starrett 1959, Marzolf and Osborne 1971, Kimmel and Lind 1972). More recently, the role of watershed-

reservoir interactions in determining the trophic structure and energy and materials flow patterns which comprise reservoir ecosystems has received increased attention (e.g., McConnell 1968, Lind 1971, Goldman and Kimmel 1978, Kimmel 1979, Marzolf 1980).

A number of investigations have related turbidity and nutrient levels to variations in phytoplankton standing crop and community composition (Chandler 1940, 1942a, 1942b, 1944; Chandler and Weeks 1945; Verduin 1951, 1954). Harris and Silvey (1940) attempted to relate phytoplankton standing crops to turbidity in several Texas reservoirs, but obtained contradictory results. Fewer studies have examined the interrelationships of turbidity caused by suspended particles, nutrient availability and phytoplankton photosynthesis rates. Turbid inflow to Lake Tahoe, one of the clearest and least productive lakes in the world, produced three primary effects on phytoplankton productivity (Tilzer et al. 1976):

- (1) Surface light inhibition of photosynthesis was reduced, and thus, near-surface productivity increased;
- (2) Light availability in deeper layers decreased, and thereby integral primary production within the water column declined;
- (3) Nutrient availability increased, and photosynthesis at depths not light limited was enhanced.

Stross and Stottlemeyer (1965) examined phytoplankton productivity in the Patuxent River estuary, and demonstrated the effect of superimposed light and nutrient availability gradients on photosynthetic production. Primary productivity per unit volume, turbidity and nutrient availability decreased from upstream to downstream stations along a 29-mile transect. However, primary productivity per unit area was greater at downstream stations due

to increased light penetration. Such superposition of light and nutrient gradients is characteristic of systems which receive turbid watershed inflow, and similar effects on phytoplankton productivity have been observed in reservoirs (e.g., Marzolf and Osborn 1971; Kimmel and Lind 1972; Thornton et al., in press).

Little research has addressed the effects of watershed inflow on bacterial activity and distribution in reservoirs, although bacterial attachment to and aggregation of suspended organic detritus particles have received much attention in the oceanographic and limnological literature (see review by Goldman and Kimmel 1978, and references therein). On the basis of laboratory experiments, Jannasch and Pritchard (1972) suggested that adsorption of dissolved organic compounds and inorganic nutrients increased concentration gradients at particle surfaces and promoted microbial attachment to particles in dilute systems. Paerl and Goldman (1972) and Goldman et al. (1974) reported microheterotrophic activity in ultra-oligotrophic Lake Tahoe to be stimulated by suspended silt particles introduced by watershed runoff. Azam and Hodson (1977) and Paerl (1980) have reported for oceanic and lake systems, respectively, that most microheterotrophic activity appears to be associated with free-living bacteria, rather than bacteria attached to or otherwise associated with larger particles. As suggested by the very small size ( $< 1 \mu\text{m}$  effective diameter) of the free-living microheterotrophs investigated by Azam and Hodson (1977) and the results of both Sorokin (1968, 1971) and Seki (1972), bacterial clumps, bacteria attached to larger particles and bacterial-detrital aggregates probably comprise the portion of the total microheterotrophic production which is most available to planktonic grazers. Although many filter-feeding



zooplankton are capable of collecting and ingesting free-living bacteria (e.g., Friedman 1977, Peterson et al. 1978, Pilarska 1977, Starkweather et al. 1979), the collection efficiency for such small particles is usually much lower than that for larger particles (Peterson et al. 1978).

The suspended matter transported into reservoirs by tributaries provides a greater number of particles and surface area for microbial attachment and heterotrophic growth than is present in most oceanic or lacustrine pelagic systems. Whether higher organic matter and nutrient concentrations in reservoirs decrease the adsorptive nutrient gradient enhancement observed by Jannasch and Pritchard (1972) in dilute oceanic systems is unknown. In the laboratory, Marzolf and Arruda (1980) have shown the possibility of a dissolved organic matter - clay - grazer food chain in reservoirs by experimentally demonstrating methionine adsorption to reservoir clay particles, assimilation of clay-adsorbed methionine by Daphnia, and successful reproduction by Daphnia fed only methionine-clay. Since microheterotrophic production is not directly light-dependent, it could contribute significantly to the organic matter base of the planktonic foodweb in light-limited, nutrient-rich systems; e.g., many midwestern reservoirs (Goldman and Kimmel 1978, Marzolf 1980). Especially in well-mixed, turbid reservoirs in which the mixed-layer depth exceeds that of light penetration, and thus, phytoplankton production is limited by both the amount of time and the frequency with which algal cells are exposed to light, microheterotrophic production could form an important portion of the particulate organic matter base of the foodweb.

The primary goal of this research was to determine the effects of nutrients and suspended soil particles, introduced via watershed runoff,

on organic matter production in receiving reservoir systems. Phytoplankton photosynthesis and microheterotrophic secondary production form the organic matter base of reservoir foodwebs (Goldman and Kimmel 1978, Kimmel 1979), and thus, are appropriate levels for evaluating ecological and water quality effects of watershed runoff. This investigation was designed to answer the following questions:

- (1) Does the introduction of silt and clay particles to the reservoir water column reduce water transparency to such a degree that phytoplankton photosynthesis becomes limited by light availability?
- (2) Does the introduction of dissolved nutrients in runoff water and desorption of nutrients from suspended silts and clays increase nutrient availability, and thereby stimulate organic matter production by phytoplankton and bacteria?
- (3) Does the presence of suspended silts and clays stimulate microbial activity by concentrating dissolved organic compounds via adsorption and then functioning as both surface and substrate for the growth of attached microorganisms?
- (4) Does turbid watershed inflow modify the availability of microheterotrophic production to grazers via bacterial attachment to or aggregation with silt and clay particles in the water column?

A combination of field and laboratory measurements and experiments were employed to address these questions.

## 2. DESCRIPTION OF THE STUDY SITE: LAKE TEXOMA

Most of the research conducted during this investigation was centered at the University of Oklahoma Biological Station and Lake Texoma (Oklahoma-Texas). However, some field evaluation of methodologies was conducted at Broken Bow Lake (southeastern Oklahoma) and Lake Murray (southcentral Oklahoma), and 1979 watershed runoff experiments were performed at the U.S. Department of Agriculture Southern Plains Watershed and Water Quality Laboratory (Durant, Oklahoma) in cooperation with O.R. Lehman. Because it was the primary focus of this project, only Lake Texoma will be described here.

Lake Texoma is a large storage reservoir located on the Oklahoma-Texas border at the confluence of the Red and Washita Rivers (Fig. 1). The lake was impounded by the U.S. Army Corps of Engineers in 1942, and reached power pool level in 1944. The reservoir is the key unit in the Red River basin plan for flood control (affecting Texas, Oklahoma, Arkansas and Louisiana), power generation, water supply, stream-flow regulation and navigational improvement of the lower Red River. Lake Texoma is the third most heavily used Corps of Engineers impoundment in the U.S. (ca. 12 million visitors annually) and represents a major resource for tourism and recreation. The Lake Texoma watershed encompasses 103,000 km<sup>2</sup> (40,000 mi<sup>2</sup>) and includes much of southwestern Oklahoma, the Texas panhandle and a portion of eastern New Mexico (Fig. 2). The Red and Washita Rivers contribute approximately 70% and 30% of the annual inflow, respectively. During high flow periods, both tributaries acquire heavy sediment loads in draining extensive areas of highly erodable soils. Saline inflow to the Red River via natural sources (salt-rich Permian deposits, saline springs, groundwater seeps,

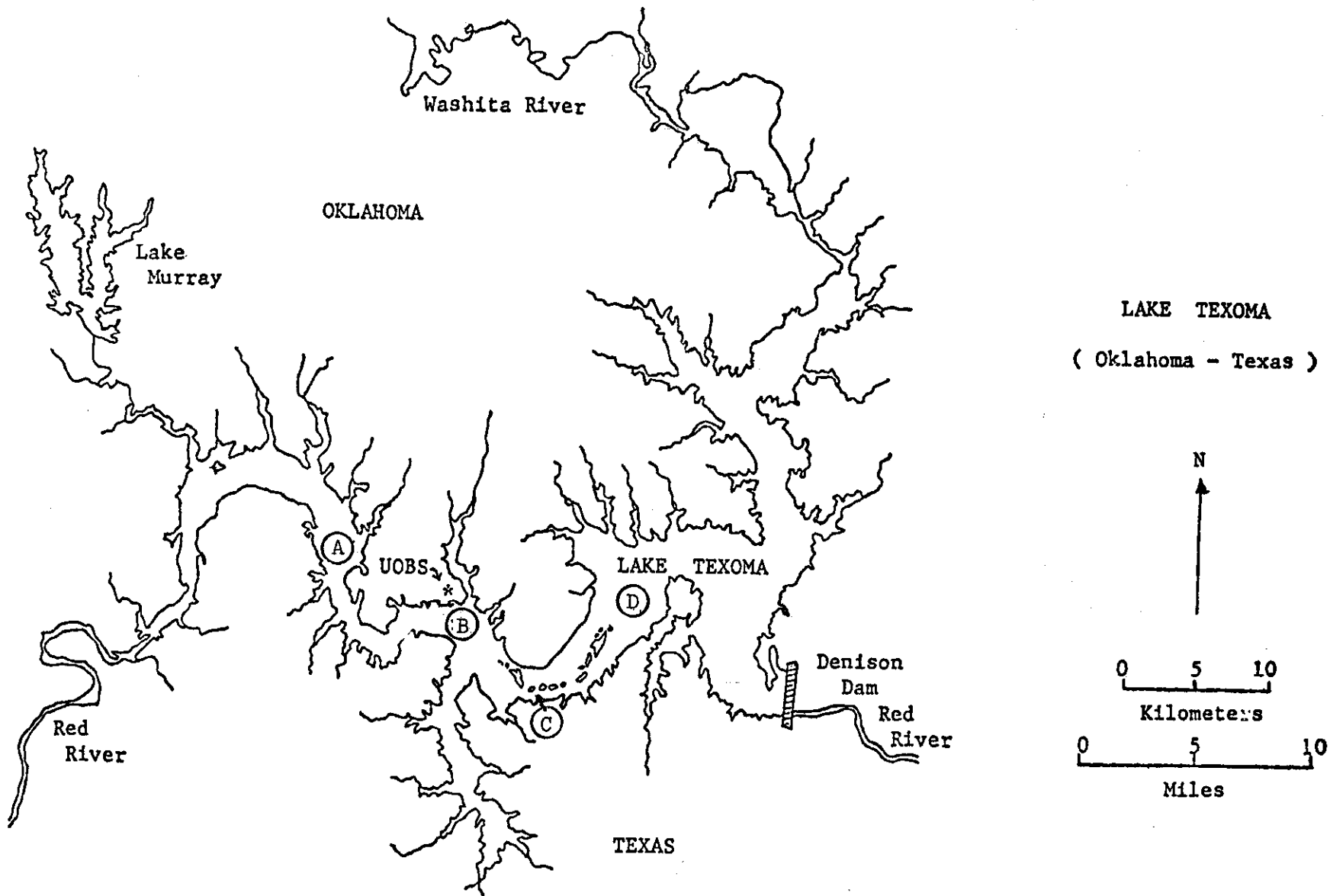


Fig. 1. Map of the study site, Lake Texoma (Oklahoma-Texas). The location of the University of Oklahoma Biological Station (UOBS) is marked by an asterisk. Sampling stations are indicated by letters: A (uplake station), B (UOBS station), C (channel station) and D (downlake station).

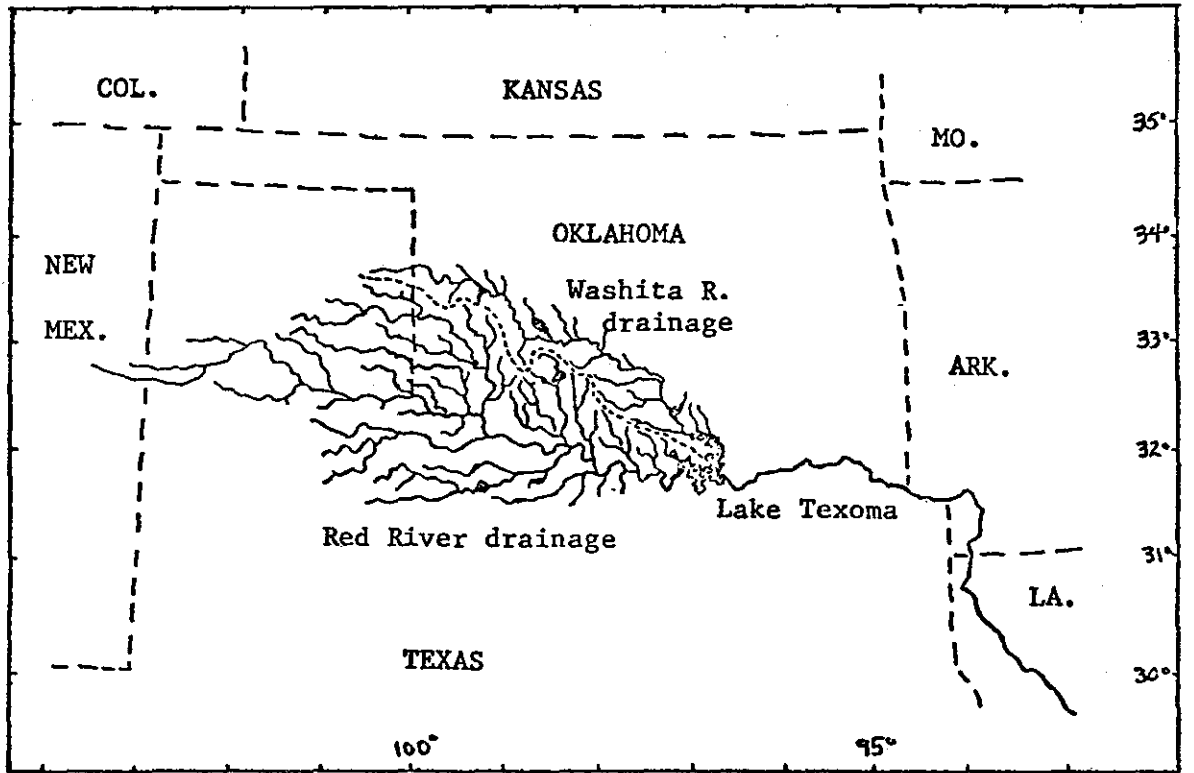


Fig. 2. Drainage basin of Lake Texoma (Oklahoma-Texas).

and salt flats) occurs in tributary headwaters, and the Red River inflow to Lake Texoma may exceed 1 ppt salinity during low-flow periods. Although it is among the larger water bodies in the nation, Lake Texoma remains relatively unused for water supply due to its high dissolved salt content. However, Lake Texoma water is included in both Oklahoma and Texas water plans for transfer to arid western portions of those states, and so, may be utilized in the future.

Lake Texoma is representative of large, multiple-use impoundments of the U.S. Great Plains (see Table 1 for morphometric data). Vigorous wind-mixing of the water column, low water transparency (0.5 - 2.0 m Secchi depth), high dissolved salt levels (400-2000  $\mu\text{mhos cm}^{-1}$  conductance), high mid-summer water temperatures (28-32 °C), moderate lake level instability (annual water level fluctuation = 3-4 m) due to flood control and hydro-power operations, and high biological productivity are characteristic features. Lake Texoma is eutrophic, with phytoplankton productivity in near-surface waters often exceeding  $50 \text{ mg C m}^{-3} \text{ hr}^{-1}$  of mid-day incubation (equivalent to ca.  $500 \text{ mg C m}^{-2} \text{ day}^{-1}$ ) in mid-summer. Although potential nuisance algae (Aphanizomenon, Anabaena and Microcystis) have been dominant components of the phytoplankton community for at least 30 years (Sublette 1955), algal bloom problems are infrequent. Lake Texoma has been biologically productive since the time of its impoundment, and continues to support an excellent sport fishery.

Table 1. Morphometric characteristics of Lake Texoma at conservation pool level.

	Metric Units	English Units
Date Impounded	1944	1944
Surface Elevation (MSL)	188 m	617 ft
Surface Area ( $A_o$ )	360 km <sup>2</sup>	89,000 acres
Volume	3.36 x 10 <sup>9</sup> m <sup>3</sup>	2,733,000 ac-ft
Total Annual Discharge	4.25 x 10 <sup>9</sup> m <sup>3</sup>	3,446,000 ac-ft
Theoret. Renewal Time	288 days	288 days
Mean Depth	9 m	31 ft
Maximum Depth	34 m	115 ft
Outflow Depth	29 m	95 ft
Shoreline Length	933 km	580 mi
Shoreline Development	13.9	13.9
Drainage Basin Area ( $A_d$ )	103 x 10 <sup>3</sup> km <sup>2</sup>	39,719 mi <sup>2</sup>
$A_d : A_o$ Ratio	286	286

### 3. METHODS AND MATERIALS

#### 3.1. General Methods

A combination of physical, chemical and biological measurements were conducted routinely during experiments and in the field. Water temperature, dissolved oxygen, pH and conductance were measured in situ with a Hydrolab Surveyor unit. Photosynthetically-active solar radiation (PAR, 400-700 nm) and relative light penetration were determined with a quantum sensor (Li-Cor 185A). Relative water transparency was estimated via Secchi disc reading. Water samples were obtained with either a 3-l or an 8-l opaque plastic Van Dorn sampler.

Dissolved  $\text{PO}_4\text{-P}$  and  $\text{NH}_4\text{-N}$  analyses were by the phosphomolybdate and phenolhypochlorite methods, respectively (Strickland and Parsons 1972).  $\text{NO}_3\text{-N}$  was determined by a modified hydrazine reduction method (Kamphake et al. 1967). Microbial biomass was estimated from adenosine triphosphate (ATP) levels as determined by the luciferin-luciferase assay (Holm-Hansen and Booth 1966). Chlorophyll a concentrations were determined spectrophotometrically after grinding and extraction of filtered samples in 90% acetone (Strickland and Parsons 1972). Phytoplankton productivity was estimated by the  $^{14}\text{C}$  method of Steeman Nielsen (1952) as modified by Goldman (1963). Dissolved inorganic carbon availability for photosynthetic uptake was derived from temperature, pH and total alkalinity data (Saunders et al. 1962).

#### 3.2. In Vivo Chlorophyll Fluorescence and Phytoplankton Photochemical Capacity

##### Laboratory Experiments

In vivo chlorophyll fluorescence parameters and photosynthesis rates



of reservoir phytoplankton assemblages were compared in laboratory light-deprivation experiments. Near-surface Lake Texoma water was strained through 80- $\mu$ m netting to remove large zooplankton, placed in a 4-l, foil-covered Pyrex flask and incubated with gentle-stirring at 25°C. Subsamples were removed periodically for photosynthesis and in vivo fluorescence measurements.

Photosynthesis rates were determined by radiocarbon uptake in 125-ml Pyrex light and dark bottles. Samples were inoculated with 1.0  $\mu$ Ci  $\text{NaH}^{14}\text{CO}_3$  solution, incubated for 4 hrs at 25°C and 64  $\mu\text{E m}^{-2} \text{sec}^{-1}$ , and then vacuum-filtered on Whatman GFC filters. Sample activity was determined by liquid scintillation spectrometry (Beckman LS 8000).

In vivo chlorophyll fluorescence was measured with an AMINCO fluorocolorimeter equipped with a blue excitation lamp (GE F4T5-B, 4 W  $\text{m}^{-2}$  intensity), Corning glass primary (No. 5543) and secondary (No. 2030) filters, RL36 photomultiplier tube and an integrator-timer. Fluorescence of unpoisoned and DCMU-poisoned<sup>1</sup> samples was determined over 5-sec integration periods initiated simultaneously with sample excitation for each of triplicate subsamples. The fluorescence of an unpoisoned 5-ml sample was determined, 0.2 ml of  $10^{-4}$  M DCMU solution added with an automatic micropipet (final DCMU concentration =  $10^{-5}$  M), the sample mixed by inverting the cuvette several times, and fluorescence of the poisoned sample measured. Preliminary experiments showed that 1-hr dark storage, 5 min following DCMU addition, and 20 sec between excitation periods were sufficient intervals for avoiding photo-

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<sup>1</sup> DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea) prevents reoxidation of the Q intermediate, and thereby blocks non-cyclic electron transport from Photosystem II and the oxidation of water (i.e., the Hill reaction).

inhibition effects, allowing DCMU penetration of cells and permitting cellular fluorescence recovery between readings, respectively. Sufficient dark storage time (at least 30 min) is particularly important in order to remove any bright-light depression of fluorescence (PS II - PS I spillover) and ensure that all cells are in light state 1 (Vincent 1979, 1980).

#### Field Measurements

Water column samples for fluorescence measurements were obtained with an opaque Van Dorn sampler and drained into opaque 1-l PVC bottles for transport to the laboratory. Care was taken to avoid exposure of samples to surface light. All other field data were obtained by methods described in Section 3.1. In situ sample displacement experiments, in which photosynthetic  $^{14}\text{C}$  uptake was measured in samples obtained from several water column depths (and light intensities) and incubated at a single depth, were conducted to provide an independent measure of phytoplankton photosynthetic potential for comparison to in vivo chlorophyll fluorescence data.

#### Expression of DCMU-Enhanced Fluorescence Results

Previous investigators have used a variety of methods for indicating in vivo chlorophyll fluorescence response to DCMU poisoning, with most employing some ratio of the unpoisoned initial fluorescence to either DCMU-enhanced fluorescence or extracted chlorophyll. Sample fluorescence yield depends on both algal physiological state and the amount of chlorophyll present. Slovacek and Hannan (1977) concluded that DCMU-enhanced fluorescence corresponded closely to total (extracted) chlorophyll for a variety of algal species and growth conditions. I was interested in evaluating

fluorescence response as an indicator of algal physiological status, and chose to express results in terms of FRI values (previously used by Kiefer and Hodson 1974, Cullen and Renger 1979), where:

$$\frac{F_d - F_i}{F_d} = \text{FRI}$$

and  $F_i$  = initial (unpoisoned) sample fluorescence,

$F_d$  = DCMU-poisoned sample fluorescence, and

FRI = the fluorescence response index for the phytoplankton assemblage sampled.

For my purposes, FRI possessed two major advantages:

- 1) FRI should be relatively biomass-independent (i.e., normalized relative to  $F_d$  = algal chlorophyll) and thus, should reflect the average physiological state (or photochemical capacity) of the phytoplankton assemblage, and
- 2) FRI has a theoretical range of 0 ( $F_d - F_i = 0$ , no photosynthetic electron transport activity) to 1.0 ( $F_i = 0$ , all absorbed energy involved in photosynthetic electron transport).

### 3.3. Bioassay Experiments

#### Nutrient Enrichment Bioassay

Preliminary nitrogen and phosphorus bioassay experiments were conducted in mid-summer 1979 to (i) determine if Lake Texoma phytoplankton assemblages experienced nutrient limitation, and if so, (ii) to identify the primary limiting nutrient. Inorganic nitrogen ( $\text{NO}_3\text{-N} + \text{NH}_4\text{-N}$  in equal portions, total N enrichment =  $400 \mu\text{g N l}^{-1}$ ) and phosphorus ( $\text{PO}_4\text{-P}$ , total P enrichment =  $400 \mu\text{g P l}^{-1}$ ) were added to Lake Texoma near-surface samples from uplake and downlake stations (A and D, respectively; see Fig. 1 for station

locations) in acid-washed 500-ml Pyrex culture flasks. Controls received no nutrients. All treatments (total of 8, including controls) were duplicated and samples were incubated outside in a shallow bioassay pool through which Lake Texoma mixed-layer water was circulated. Enriched subsamples and controls were monitored via in vivo chlorophyll fluorescence methods (see Section 3.2) to assess the effects of N and P additions on algal biomass and photochemical capacity.

#### Soil-Nutrient Enrichment Bioassay

In 1980, unfiltered Lake Texoma surface water samples were experimentally enriched with simulated watershed runoff of two types, San Saba clay and Bowie loam, and with filtered runoff (i.e., containing nutrients and organic compounds leached from the soils, but no soil particles). These experiments were designed to separate dissolved and particle-bound nutrient enrichment effects, and particle surface effects on autotrophic and microheterotrophic activities. Treatments were:

- 1) Soil + nutrients, San Saba clay:  $(S + N)_{SSC}$
- 2) Leached nutrients only, San Saba clay:  $(N)_{SSC}$
- 3) Soil + nutrients, Bowie loam:  $(S + N)_{BL}$
- 4) Leached nutrients only, Bowie loam:  $(N)_{BL}$
- 5) Control, 80- $\mu$ m screened lake water only: C

Twenty-five grams of fine San Saba clay or Bowie loam soil (passed through a Tyler No. 20 sieve, 841  $\mu$ m diameter) was suspended in 1200 ml 80- $\mu$ m screened Lake Texoma water in 2000-ml Pyrex graduated cylinders. No soil was added to controls, and all treatments were duplicated. All systems were shaken and resettled repeatedly in the laboratory over a 4-day period to promote establishment of a nutrient adsorption-desorption equi-

librium. Following the equilibration period, an 800-ml subsample was removed from each system and mixed thoroughly with 3000 ml of 80- $\mu$ m screened lake water in 4-l translucent plastic cubitainers. Control and (S + N) treatments were thoroughly shaken to resuspend settled particles prior to dispensing the 800-ml aliquot, while 800 ml were carefully siphoned from undisturbed systems to avoid inclusion of suspended particles in nutrients-only (N) treatments. Cubitainers were floated at the surface of an outdoor bioassay tank through which water from the Lake Texoma mixed layer was circulated. Thus, the bioassay systems were exposed to natural summer light:dark cycles, and mixed-layer light intensities (the translucent plastic cubitainers reduced surface light intensity by ca. 90%) and temperatures. Changes in algal biomass and photochemical capacity were monitored by measurement of in vivo chlorophyll fluorescence and fluorescence response to DCMU, as described above.

#### 3.4. Size Distribution of Autotrophy and Microheterotrophy

The size distribution of planktonic autotrophy and microheterotrophy was determined by combining double-isotopic labelling of naturally-occurring phytoplankton-bacterial assemblages and size-fractionation filtration procedures. Upon return to the laboratory, water column samples were dispensed into duplicate 125-ml light and dark bottles, inoculated with 0.5 ml of 4.72  $\mu$ Ci ml<sup>-1</sup> NaH<sup>14</sup>CO<sub>3</sub> solution (specific activity = 59.3  $\mu$ Ci mmole<sup>-1</sup>) and 0.2 ml of 25  $\mu$ Ci ml<sup>-1</sup> <sup>3</sup>H- sodium acetate (specific activity = 2 Ci mmole<sup>-1</sup>; sodium acetate enrichment over ambient concentration = 1.65  $\mu$ g l<sup>-1</sup>), and incubated for 2-4 hrs at 60  $\mu$ E m<sup>-2</sup> sec<sup>-1</sup> and 28°C. Control samples in

125-ml light bottles were poisoned with 1 ml saturated  $\text{HgCl}_2$  solution prior to injection of isotopes, and then incubated along with the light and dark samples. Poisoned controls permitted correction for adsorption of radioisotopes to suspended particles in the sample and to filters. On one occasion,  $^{14}\text{C}$ -sodium acetate was used to assess microheterotrophic activity and incubations were conducted in situ.

Following incubation, double-labelled samples were size-fractionated by gentle filtration ( $< 0.33$  atmos vacuum pressure) of 5-to-20 ml aliquots (depending on particulate matter concentrations) through Nucleopore polycarbonate filters of specified pore diameters. Usually 0.2, 0.8, 3.0 and 8.0- $\mu\text{m}$  pore diameter filters were used, although filter sizes were varied somewhat. Filters and retained particulate matter were placed in plastic mini-vials (scintillation grade), dried in a desiccator at room temperature and pressure, and 6 ml PCS fluor (Amersham-Searle) added.

The  $^{14}\text{C}$  and  $^3\text{H}$  activities of samples retained on each filter were determined by liquid scintillation spectrometry (Beckman LS 8000). All counts were corrected for adsorption of  $^{14}\text{C}$  and  $^3\text{H}$  to filters and particulate matter by subtraction of the activities of control (poisoned) samples. Results are expressed as the percent activity retained by various filters as compared to the "total" retained by the 0.2 or 0.4  $\mu\text{m}$  filter; i.e.,

$$\% \text{ retention by filter of pore size, } n = \frac{\text{dpm retained by filter } n}{\text{dpm retained by } 0.2 \mu\text{m filter}} \times 100$$

### 3.5. Simulated Watershed Runoff Experiments

Experiments were conducted at the U.S. Department of Agriculture Southern Plains Watershed and Water Quality Laboratory (USDA SPWWQL; Durant, Oklahoma) in 1979, and at the University of Oklahoma Biological Station (UOBS) on Lake Texoma in 1980. Light availability, phytoplankton carbon uptake rates, algal biomass and phytoplankton fluorescence response were monitored during experimental enrichments of isolated water columns (in model ponds at the USDA SPWWQL, and in Lake Texoma at the UOBS) with simulated San Saba clay and Bowie loam runoff. Clear polyethylene cylinders (USDA SPWWQL: 0.5 m diameter, 2.5 m deep, sealed at bottom; UOBS: 1.5 m diameter, 2.5 m deep, sealed at bottom) were used to isolate water columns for experimental purposes (see Goldman 1962, Kimmel and Lind 1972), and filled with water via electric pump. Collars of cylinders extended above the water surface to prevent water exchange. In all cases, the runoff mixture was added gently to the surface layer of the isolated water column to simulate a turbid overflow condition. Control water columns received no runoff addition.

### 3.6. In Situ Effects of Turbid Watershed Inflow

Intensive field measurements were made during inflow pulses to the Red River arm of Lake Texoma in 1978, 1979 and 1980. All methods employed are described above.

#### 4. RESULTS AND DISCUSSION

##### 4.1 Evaluation of DCMU-Enhanced In Vivo Chlorophyll Fluorescence as an Indicator of Phytoplankton Physiological Status

Photosynthesis researchers have employed the herbicide, DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea), in experimental investigations of the photochemical processes occurring in green plant cells for almost two decades. The maximal in vivo fluorescence and lack of photosynthetic oxygen evolution observed when algae or other plant cells are exposed to light in the presence of DCMU has been attributed to DCMU-blocking of non-cyclic photosynthetic electron transport and the subsequent dissipation of much of the energy of excited chlorophyll molecules by fluorescence (Duysens and Sweers 1963). Although the quantum yield of energy absorbed by the reaction centers of Photosystem II can be dissipated by several competing de-excitation processes (i.e., photochemical activity, fluorescence from Photosystem II, spillover from Photosystem II to Photosystem I, or radiationless transfer), a complementary relationship to photosynthetic activity and in vivo chlorophyll fluorescence has often been observed (e.g., Butler 1966, Goedheer 1972, Papageorgiou 1975). Such correspondence suggests (i) a partial explanation for the variability of fluorescence yield (fluorescence per unit chlorophyll) observed for both algal cultures and natural phytoplankton assemblages (i.e., variable photosynthetic activity, thus, variable fluorescence yield), (ii) the potential usefulness of DCMU for reducing the variability of in vivo chlorophyll measurements, and (iii) application of the variable fluorescence response (i.e., the relative fluorescence increase induced by DCMU poisoning) as an indicator of algal photochemical capacity and thus, physiological status.



Slovacek and Hannan (1977) examined the applicability of DCMU-poisoning for maximizing the fluorescence yield of phytoplankton samples, and thereby reducing the variability of in vivo chlorophyll fluorescence estimates of algal biomass. DCMU-poisoning of samples effectively reduced dependence of in vivo chlorophyll fluorescence on environmental conditions and algal growth state, and decreased the variability of fluorescence yield. They concluded that DCMU-blocking of electron transport from Photosystem II separates chlorophyll a from its physiological function, as does chlorophyll extraction into an organic solvent. However, other investigators have had more mixed results in applying DCMU-enhanced fluorescence measurements as an indicator of algal biomass, especially for naturally-occurring phytoplankton assemblages (e.g., Esaias 1978; McMurray 1978; Prezelin 1978, Frey 1979, Slovacek 1978, 1979, Harris et al. 1979). Esaias (1978) observed little improvement in variability of fluorescence yield in a comparison of unpoisoned and DCMU-poisoned measurements using parallel continuous-flow fluorometers. Slovacek (1978) noted similar difficulties, but suspected that at least part of the variability was attributable to the continuous-flow system. White (1980)<sup>1</sup> found that although DCMU-enhanced fluorescence provided some increase in analytical sensitivity at lower chlorophyll levels, the in vivo fluorescence of both poisoned and unpoisoned phytoplankton samples was highly correlated with extracted chlorophyll a, and therefore, either method provided an excellent estimator of algal biomass.

Halldal and Halldal (1973), Samuelsson and Oquist (1977) and Heaney (1978) suggested that the variable nature of in vivo chlorophyll fluorescence

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<sup>1</sup> Research accomplished via partial support from this OWRT project (A-088-OKLA).

might be used to an advantage in the investigation of phytoplankton physiological state. By virtue of the approximate complementarity of photosynthetic activity and in vivo chlorophyll fluorescence, an indication of the average physiological status of a phytoplankton assemblage should be possible by comparison of the in vivo fluorescence (unpoisoned) and the maximum (DCMU-enhanced) fluorescence. Samuelsson and Oquist (1977) and Samuelsson et al. (1978) reported a correspondence of DCMU-induced fluorescence increases and photosynthetic <sup>14</sup>C uptake in algal cultures, and emphasized the potential application of the technique to the investigation of natural phytoplankton assemblages.

A direct method for assessing the in situ physiological status of naturally-occurring phytoplankton assemblages would be invaluable for examining factors influencing phytoplankton productivity, biomass accumulation, spatial distribution, and bloom development and decline. Currently, it is necessary to make both primary productivity measurements and chlorophyll extractions to obtain information on algal photosynthetic capacity or physiological state. Therefore, as part of this research, laboratory and field evaluations of the DCMU-enhanced in vivo fluorescence response as an indicator of in situ phytoplankton physiological status were conducted. Specific research objectives were:

- 1) to test in vivo chlorophyll fluorescence response to DCMU-poisoning as an indicator of phytoplankton photochemical capacity / physiological state,
- 2) to determine the range of fluorescence response values to be expected in a variety of limnological conditions, and
- 3) to evaluate the utility of the fluorescence response technique for investigating factors controlling phytoplankton productivity in situ.

### Light Deprivation Experiments

The correspondence of in vivo chlorophyll fluorescence response to DCMU-poisoning and photosynthetic  $^{14}\text{C}$  uptake was tested in laboratory light deprivation experiments designed to simulate the physiological decline experienced by algal cells settling into aphotic portions of the water column. Photosynthetic carbon fixation and fluorescence parameters declined in a parallel manner; both  $^{14}\text{C}$  uptake and FRI decreased rapidly during the initial 24 hrs of darkness and then declined more gradually (Fig. 3). Relative DCMU-induced enhancement of in vivo chlorophyll fluorescence was directly related to photosynthetic carbon fixation in both experiments (Fig. 4), thus demonstrating that the fluorescence response to DCMU reflects changes in phytoplankton photochemical capacity and physiological state, at least in the laboratory.

### Field Measurements

In vivo chlorophyll fluorescence parameters and limnological measurements were compared in three limnologically dissimilar Oklahoma reservoirs in order to examine the applicability of fluorescence response methods to field studies. Lake Texoma (see Section 2 for description) is representative of many wind-swept reservoirs of the U.S. Great Plains. It is nutrient-rich, productive and well-mixed; thermal stratification is usually transitory. The euphotic layer is shallow (Secchi depth = 1 m,  $1\% I_0 = 3.5$  m) and exceeded in depth by the mixed layer. Figs. 5 and 6 reflect typical late-spring and late-summer limnological conditions. On May 28 (Fig. 5), fluorescence, dissolved nutrients and physical-chemical measurements showed the mixed layer to be 8-9 m deep. In contrast, the euphotic zone ( $> 1\%$  surface light intensity) was less than 4 m deep; and thus, the ratio of

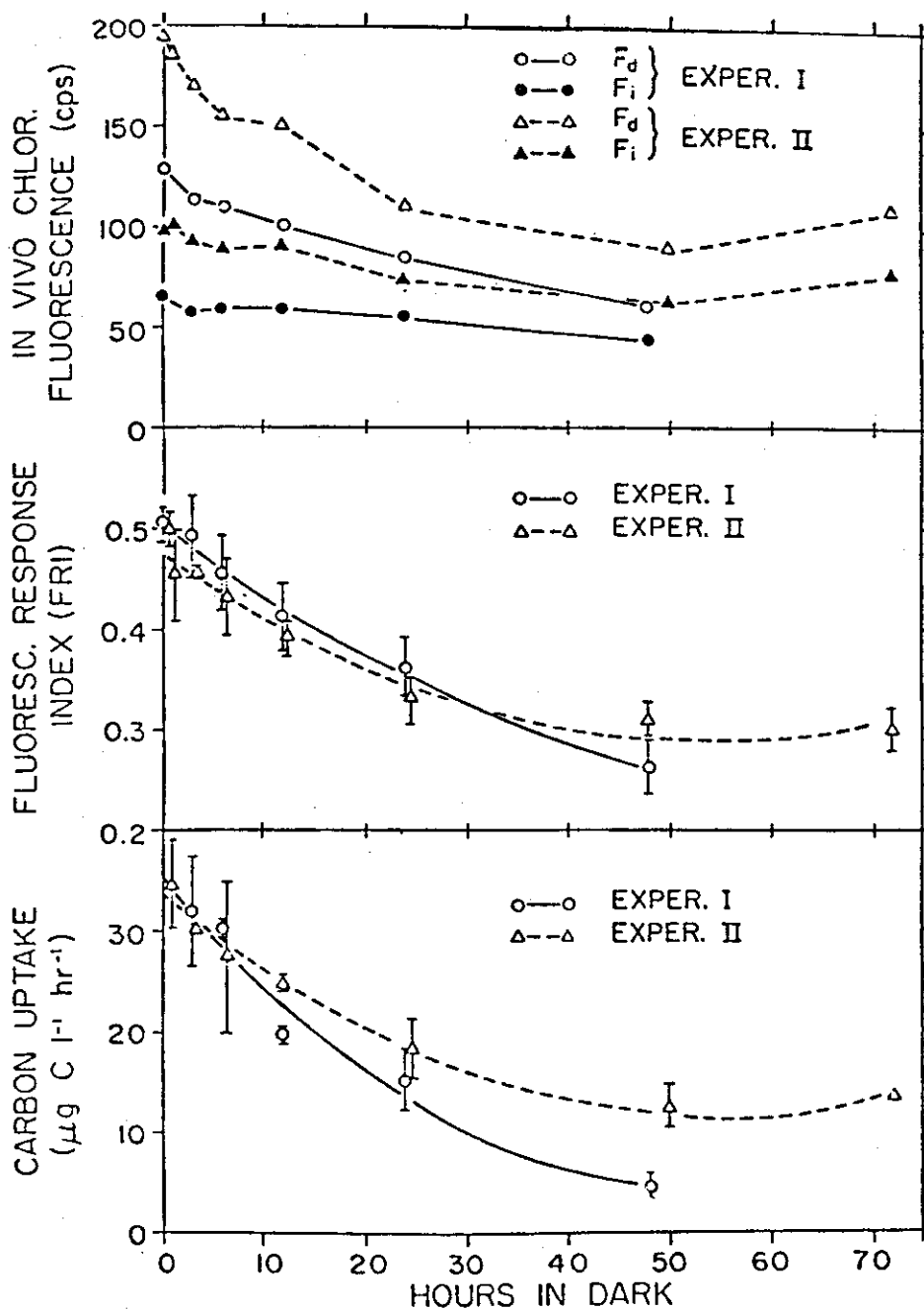


FIGURE 3. Decline of in vivo chlorophyll fluorescence ( $F_i$  = unpoisoned sample fluorescence,  $F_d$  = DCMU-poisoned sample fluorescence), the fluorescence response index (FRI) and photosynthetic carbon uptake in Lake Texoma phytoplankton assemblages during light-deprivation experiments.

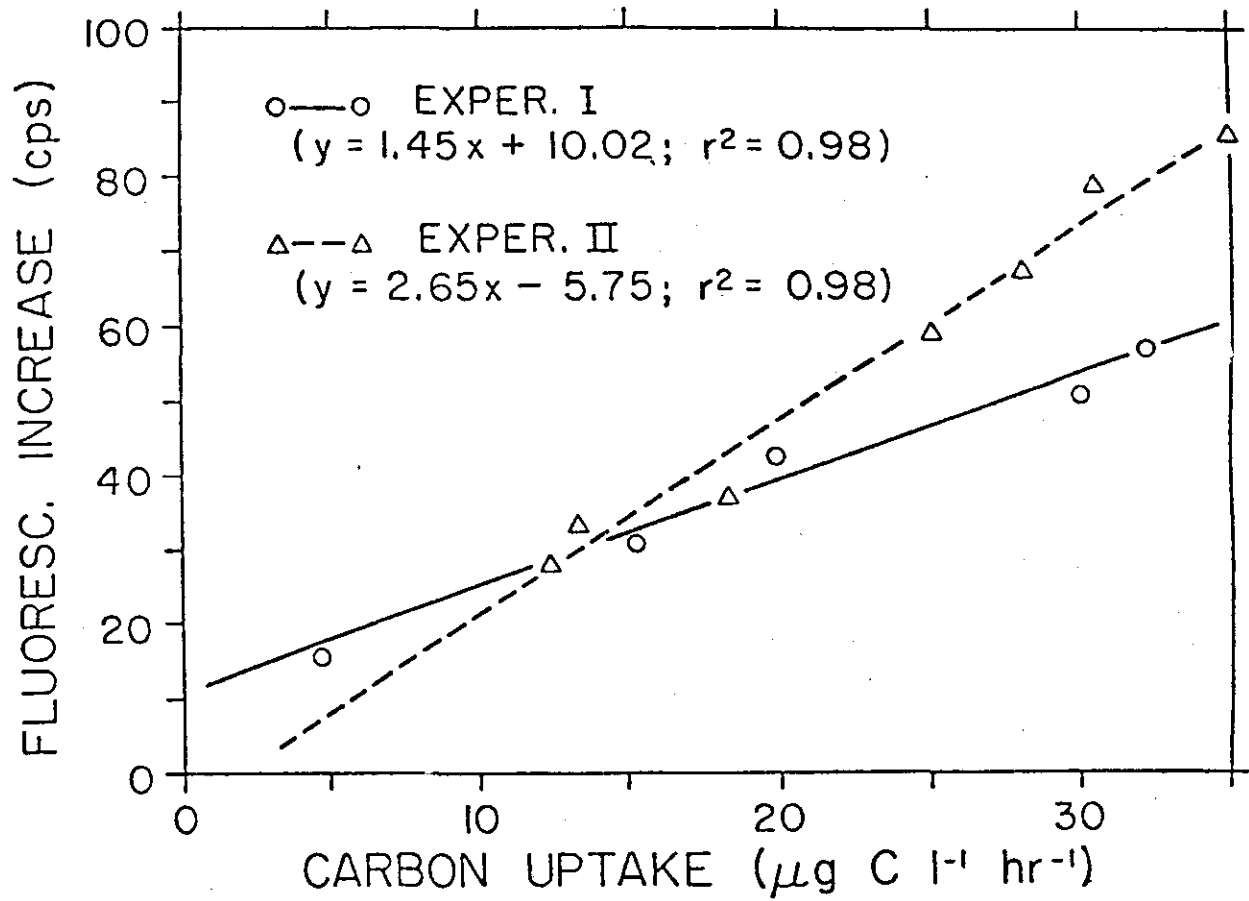


FIGURE 4. Relation between sample fluorescence increase ( $F_d - F_i$ ) and photosynthetic carbon uptake in light-deprivation experiments conducted with Lake Texoma phytoplankton assemblages.

## LAKE TEXOMA (OKLA.-TEXAS); 28 MAY 1978

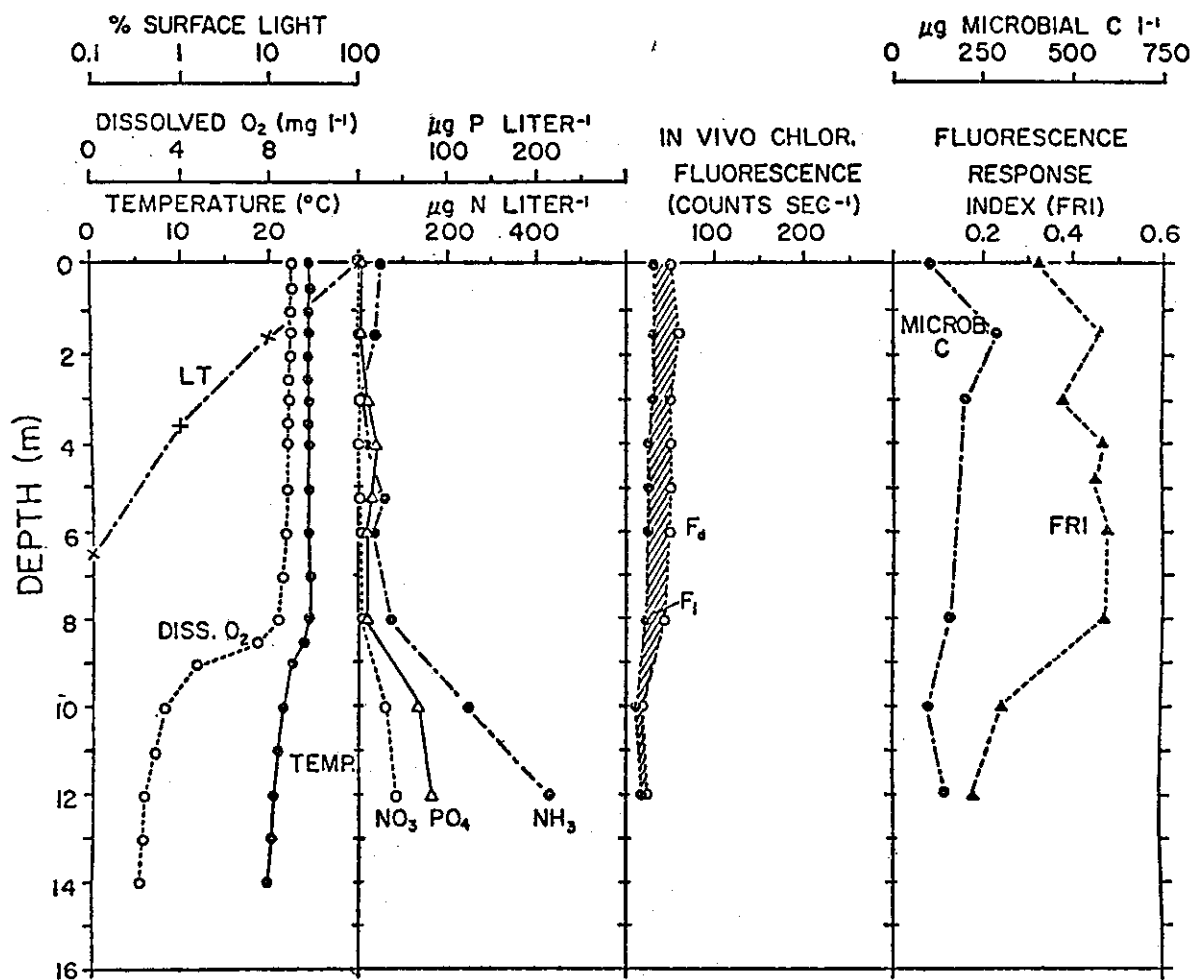


FIGURE 5. Early-summer vertical profiles of physical, chemical and biological characteristics, in vivo chlorophyll fluorescence, and the fluorescence response index (FRI) in Lake Texoma. Note the correspondence of the FRI with the extent of the mixed layer as indicated by dissolved oxygen, temperature and nutrient profiles. Also note the extent of the euphotic layer as indicated by the depth at which 1% surface light occurs.

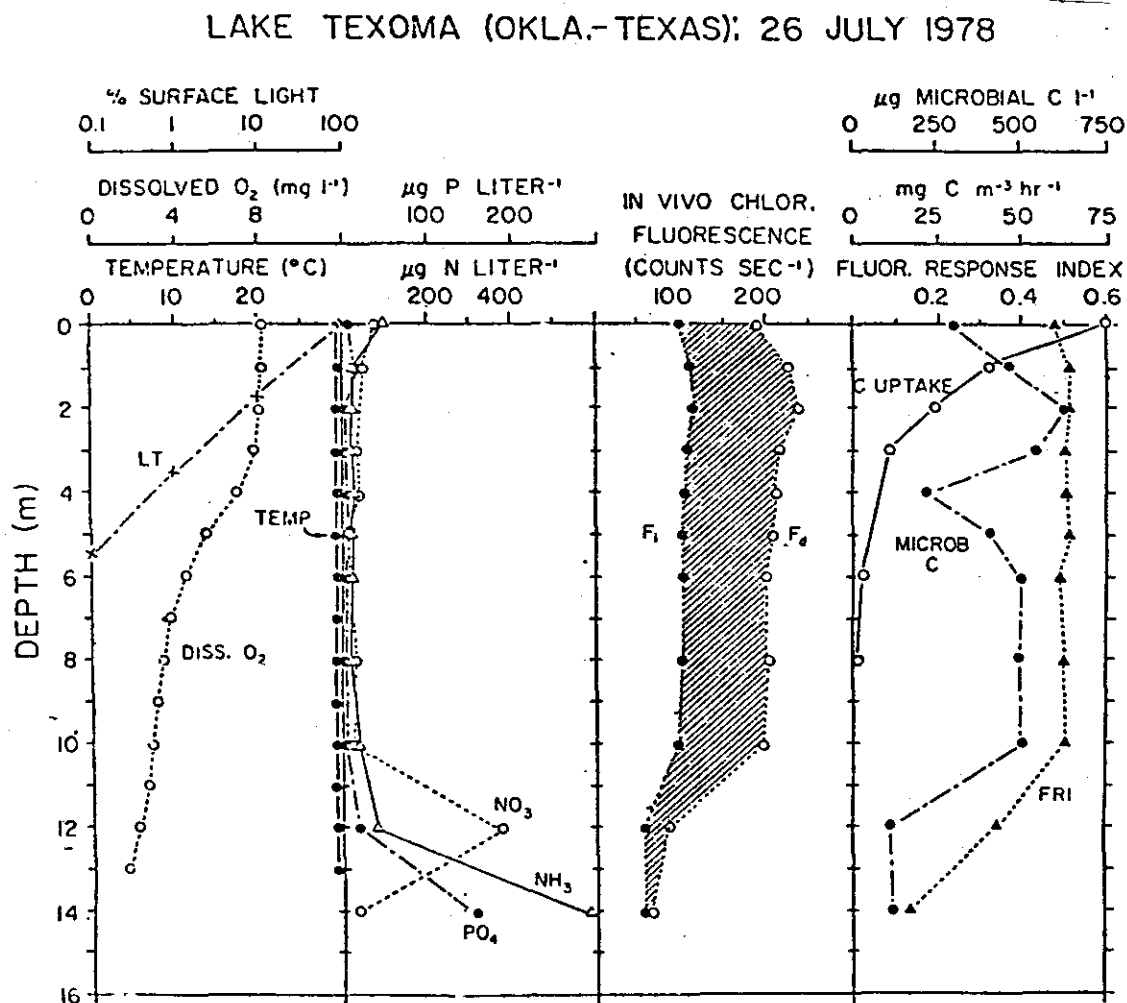


FIGURE 6. Late-summer vertical profiles of physical, chemical and biological characteristics, *in vivo* chlorophyll fluorescence, and the fluorescence response index (FRI) in Lake Texoma. Note the lack of thermal stratification; the extent of the mixed layer as indicated by nutrient,  $F_d$  and FRI profiles; and the disparity of algal biomass (as reflected by  $F_d$ ) and photosynthetic potential (as reflected by FRI) profiles to light and productivity distributions.

the euphotic layer depth ( $Z_{eu}$ ) to the mixed layer depth ( $Z_m$ ) = 0.5. Although temperature and dissolved oxygen data do not clearly indicate the extent of mixing on July 26 (Fig. 6), vertical profiles of dissolved nutrients, in vivo fluorescence and FRI show the mixed layer depth to be 10-12 m, again greatly exceeding the euphotic depth ( $1\% I_0 = 3.5$  m,  $Z_{eu} : Z_m = 3.5 : 11 = 0.32$ ). The photosynthesis-depth curve, derived from in situ <sup>14</sup>C-uptake measurements, was characteristic of light-limited primary production and indicates that little photosynthesis occurs below 3-4 m.

Phytoplankton biomass (as reflected by  $F_d$ ) was high throughout the mixed layer, and consistent FRI values (0.48-0.51) between 0 and 10 m suggested that algal photochemical capacity was maintained at depths in excess of the classical euphotic and trophogenic zones as delineated by light and productivity profiles. The results of sample displacement experiments supported this hypothesis. Samples from 1, 3 and 8 m had similar biomass-specific photosynthetic carbon uptake rates when incubated at the same light intensity (Table 2). These data show that a major fraction of the viable phytoplankton biomass in Lake Texoma occurs in the aphotic portion of the mixed layer. Apparently, mixed layer circulation is sufficiently rapid that the photochemical capacity of "aphotic" phytoplankton is retained between intervals of exposure to light. Determination of vertical mixing rates in such environments is problematic; however, at mid-summer water temperatures of 30°C, circulation must be both rapid and continuous to prevent aphotic respiratory losses from deleteriously affecting the cellular carbon balance of mixed layer phytoplankton.

Lake Murray is a small (2,320 ha), relatively deep ( $\bar{z} = 8$  m), mesotrophic



Table 2. Comparison of phytoplankton photosynthetic potential as reflected by biomass-normalized photosynthetic carbon uptake ( $C$  uptake/ $F_d$ ) and DCMU-enhanced in vivo chlorophyll fluorescence (FRI) in Lake Texoma and Broken Bow Lake sample displacement experiments. Incubation depths were 1 m ( $520 \mu E m^{-2} sec^{-1}$ ) and 3 m ( $300 \mu E m^{-2} sec^{-1}$ ) in Lake Texoma and Broken Bow Lake, respectively.  $F_d$ , reflecting algal biomass, is expressed in relative units ( $counts sec^{-1}$ ).

Sampling Depth (m)	$F_d$	C Uptake ( $\mu g C l^{-1} hr^{-1}$ )	FRI	C Uptake $F_d$
<u>Lake Texoma, 26 Jul 1978:</u>				
1	226	46.86	0.51	0.21
3	215	43.25	0.50	0.20
8	202	44.66	0.50	0.22
<u>Broken Bow Lake, 14 Aug 1978:</u>				
3	19	4.04	0.38	0.21
8	47	25.14	0.41	0.54
12	30	18.89	0.46	0.64

reservoir located in a small ( $140 \text{ km}^2$ ), relatively undisturbed and protected drainage basin in southcentral Oklahoma near Ardmore. Lake Murray was sampled on March 8 1978 to determine the correspondence of fluorescence measurements to limnological characteristics in a stably-stratified system in which  $Z_{\text{eu}} > Z_{\text{m}}$  (Fig. 7). Dissolved oxygen, temperature and light profiles showed the euphotic and mixed layer depths to be 10 and 5 m, respectively ( $Z_{\text{eu}} : Z_{\text{m}} = 2.0$ , exactly the opposite relationship as found in Lake Texoma). In vivo chlorophyll fluorescence data revealed metalimnetic peaks of both algal biomass ( $F_{\text{d}}$ ) and photochemical capacity (FRI). A very high, maximal FRI (0.68) occurred below the algal biomass peak (7 m) at 10 m, the depth of 1% surface light penetration. The FRI profile indicated the presence of phytoplankton in poor physiological condition (FRI = 0.2) both at the surface (possibly severely photoinhibited) and at depths exceeding that of 0.1% surface light (16 m).

Broken Bow Lake (southeastern Oklahoma, McCurtain Co.), a 10-yr old 5,750 ha impoundment of the Mountain Fork River, is representative of deep-valley impoundments occurring throughout eastern Oklahoma, western Arkansas and southwestern Missouri. Relative to Lake Texoma, Broken Bow Lake is oligo-mesotrophic, transparent (Secchi depth = 5-6 m) and deep ( $\bar{z} = 20 \text{ m}$ ). The reservoir is thermally-stratified throughout the growing season and its euphotic zone is deeper than the mixed layer ( $Z_{\text{eu}} : Z_{\text{m}} = 2.0$ , Figs. 8 and 9). Data obtained on July 16 and August 14 1978 revealed the presence of persistent thermal stratification and a slight metalimnetic oxygen deficit. In vivo chlorophyll fluorescence and ATP determinations indicated metalimnetic concentrations of algal and total microbial biomass, and in situ phytoplankton productivity measurements showed a pronounced metalimnetic peak of

## LAKE MURRAY (OKLA.): 8 JULY 1978

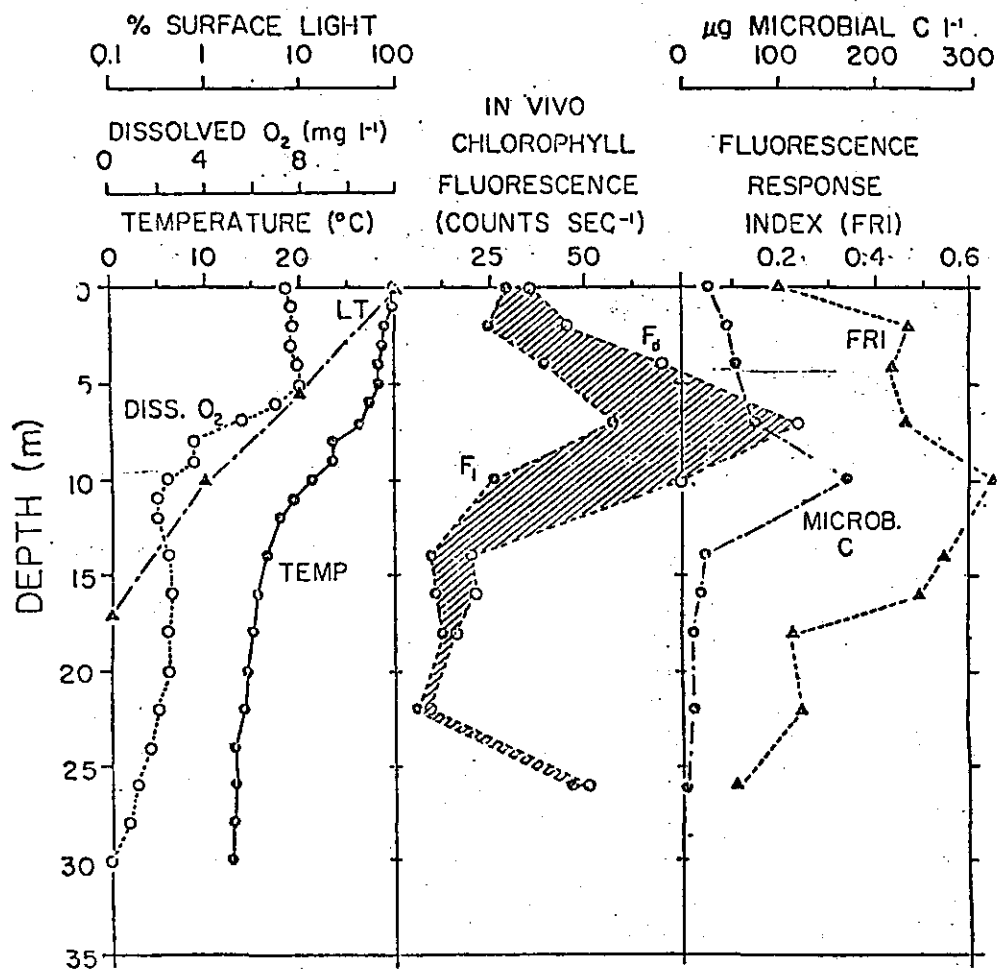


FIGURE 7. Mid-summer vertical profiles of physical, chemical and biological characteristics, *in vivo* chlorophyll fluorescence ( $F_0$ ), DCMU-enhanced chlorophyll fluorescence ( $F_d$ ), and the fluorescence response index (FRI) in Lake Murray. Note the pronounced metalimnetic peaks of algal biomass, microbial carbon, and photochemical capacity. Also note that in Lake Murray, the euphotic layer depth is greater than that of the mixed layer.

## BROKEN BOW LAKE (OKLA.): 16 JULY 1978

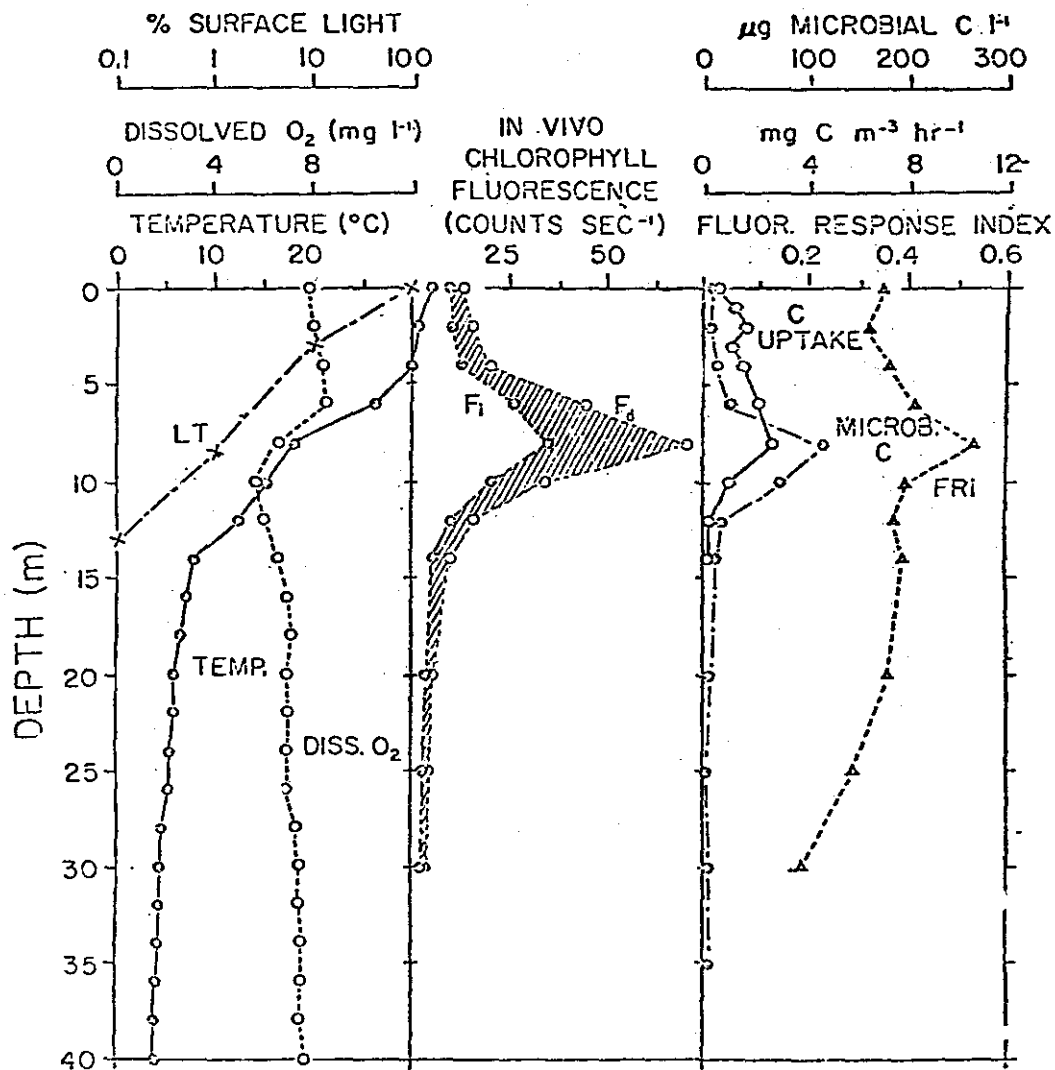


FIGURE 8. Mid-summer vertical profiles of physical, chemical and biological characteristics, *in vivo* chlorophyll fluorescence and the fluorescence response index in Broken Bow Lake. Note the correspondence of metalimnetic peaks of algal biomass (F<sub>d</sub>), microbial carbon, photosynthetic carbon uptake, and algal photochemical capacity (FRI).

## BROKEN BOW LAKE (OKLA.): 14 AUG. 1978

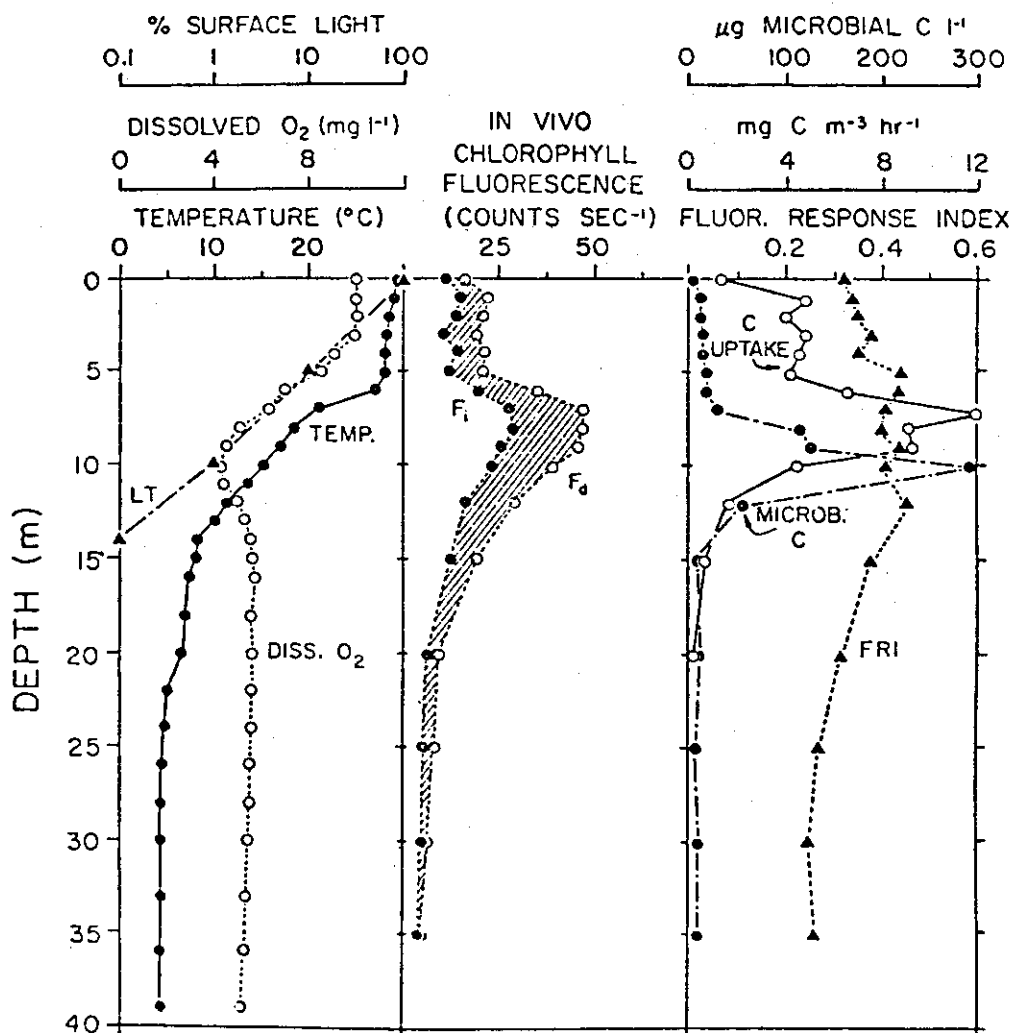


FIGURE 9. Late-summer vertical profiles of physical, chemical and biological characteristics, *in vivo* chlorophyll fluorescence, and the fluorescence response index (FRI) in Broken Bow Lake. Note the pronounced thermal stratification, metalimnetic peaks of algal biomass (as reflected by F<sub>d</sub>), microbial carbon and photosynthetic carbon uptake, and the lack of a corresponding peak in the fluorescence response index (FRI).

photosynthetic activity. Epilimnetic FRI values were low (0.32-0.39), but increased to 0.44 at 5-6 m, probably in response to greater nutrient availability near the thermocline. FRI,  $F_d$ ,  $^{14}C$  assimilation and microbial carbon all showed distinct peaks at 7 m on July 16; however, by August 14, FRI remained relatively constant (0.41-0.46) at metalimnetic depths corresponding to high algal and microbial biomass and phytoplankton productivity, and then gradually decreased below 14 m ( $= 0.1\% I_0$ ). Phytoplankton photosynthetic potential, as reflected by biomass-specific  $^{14}C$  uptake in a sample displacement experiment, again corresponded to in situ algal physiological status as indicated by FRI values (Table 2).

These field and laboratory results indicate that the chlorophyll response technique provides a rapid and convenient method for obtaining information on the in situ physiological status of naturally-occurring phytoplankton assemblages, information otherwise obtainable only by measuring both photosynthesis rates and chlorophyll concentrations. We have observed an FRI range of 0.11 to 0.68 in southern Oklahoma reservoirs and ponds. Blasco and Dexter (1972) reported FRI values of 0 and 0.6-0.7 for severely nitrogen-depleted and actively-growing algal cultures, respectively. Cullen and Renger (1979) found a similar FRI range (ca. 0 to 0.7) in continuous vertical profiling of near-shore Southern California Bight waters. Our FRI profiles corresponded well to water column characteristics and with results of experiments conducted to provide independent estimates of phytoplankton photosynthetic potential. Comparison of FRI data to rates of in situ photosynthesis in vertical profiles and displacement experiments clearly shows DCMU-enhanced fluorescence response to be an indicator of the relative photochemical capacity or physiological status of phytoplankton assemblages rather than

of in situ primary productivity, per se.

In vivo chlorophyll fluorescence remains a poorly understood phenomenon, and therefore, application of the DCMU-enhanced fluorescence method to field investigations is not free of uncertainty. Diel fluctuations in photosynthetic capacity and fluorescence response (Prezelin and Sweeney 1977), the relationship of in vivo and DCMU-induced fluorescence to algal chlorophyll (Slovacek and Hannan 1977, McMurray 1978, Esaias 1978, White 1980), and effects of community species composition (Kiefer 1973, Heaney 1978) and high light intensities (Harris 1978, 1980; Vincent 1979, 1980) on fluorescence and fluorescence response all require clarification. Therefore, DCMU-enhanced in vivo fluorescence data should be interpreted carefully, and applied only as indicative, in a relative way, of algal biomass and photochemical capacity. However, our results demonstrate that in vivo fluorescence response has utility as a physiological assay, and may be of particular value as an indicator of the extent of vertical mixing in "optically-deep" environments (sensu Talling 1957; i.e., where  $Z_{eu} < Z_m$ ). Certainly, by virtue of the simplicity of the fluorometric analysis and the integrative nature of the information obtained, DCMU-enhanced fluorescence response appears worthy of further evaluation and application in field investigations. Especially in combination with other limnological measurements and experimental techniques, the method provides a valuable tool for assessing the in situ physiological status of phytoplankton assemblages and for better understanding the environmental factors which control phytoplankton photosynthetic production under natural conditions.

#### 4.2. Enrichment Bioassays and Simulated Watershed Runoff Experiments

##### Nutrient Limitation of Lake Texoma Phytoplankton Production

Lake Texoma is both eutrophic and turbid, and light could be more limiting to algal production than nutrients. Therefore, preliminary bioassay experiments were conducted to determine if Lake Texoma phytoplankton assemblages were likely to experience nutrient limitation during mid-summer. Methods are described in Section 3.3.

Neither  $\text{NO}_3\text{-N} + \text{NH}_4\text{-N}$  or  $\text{PO}_4\text{-P}$  enrichment alone produced effects different from unenriched controls (Figs. 10 and 11). However, nitrogen and phosphorus in combination enhanced algal biomass ( $F_d$ ) and algal physiological state (FRI) in both uplake and downlake samples (see Fig. 1 for sampling locations). Station A (uplake) samples, which had a higher algal biomass initially, experienced a greater biomass increase than station D (downlake) samples; however, the physiological status of station D phytoplankton was dramatically improved from 0.19 to 0.55 FRI units. The station A phytoplankton assemblage was in good physiological condition (FRI= 0.47) at the beginning of the experiment, but increased to FRI= 0.57.

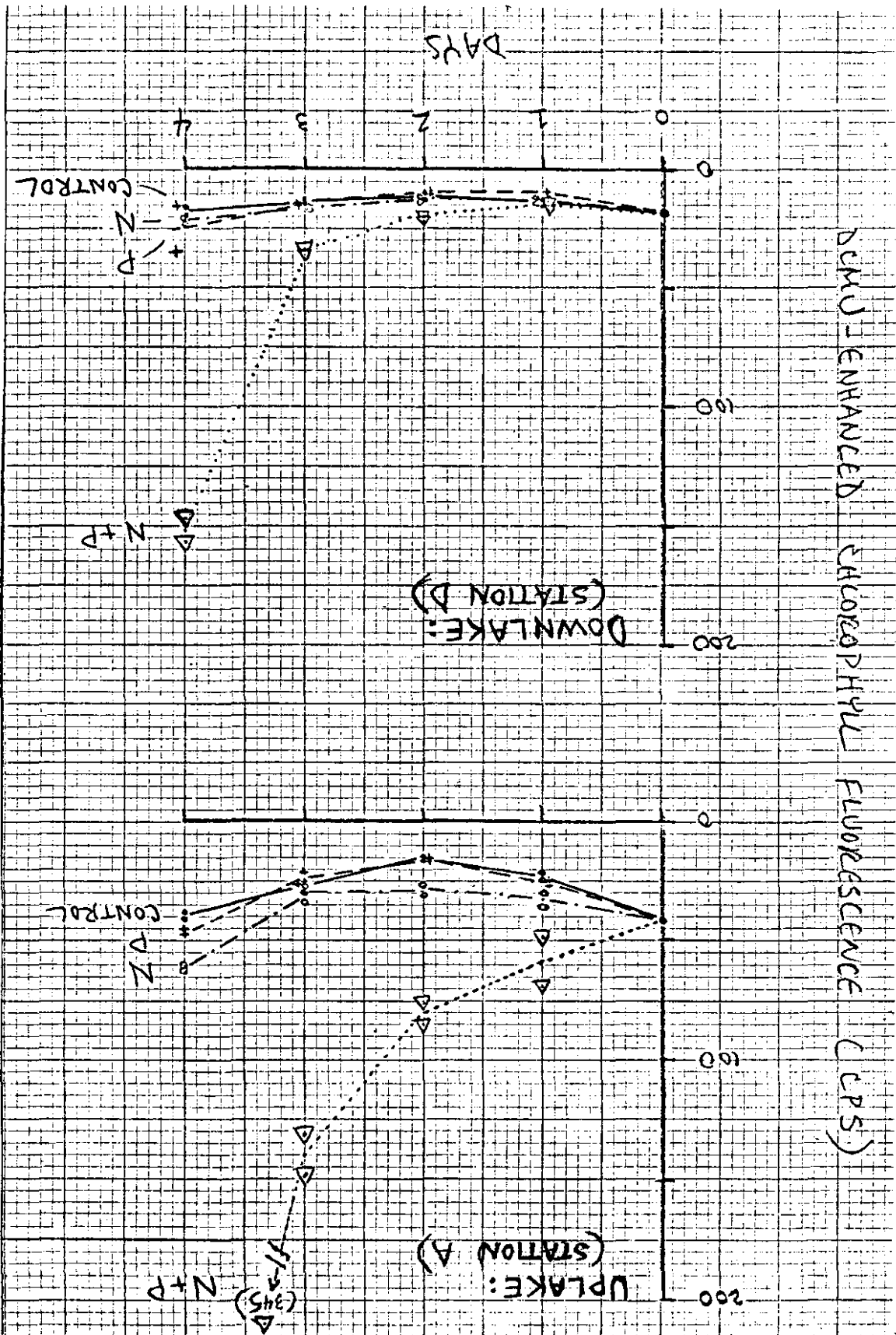
These results indicate that mid-summer phytoplankton assemblages in Lake Texoma are subject to potential nutrient limitation (by both N and P) in addition to limitation by light availability. In terms of algal physiological response, downlake phytoplankton appeared to be more nutrient-stressed than uplake communities in closer proximity to tributary inflow points; however, both uplake and downlake assemblages responded to nutrient enrichment.

##### Simulated Watershed Runoff Experiments

During the spring and summer of 1979, O.R. Lehman conducted a series of



Figure 10. Phytoplankton biomass response (as reflected by F<sub>4</sub>) to experimental nitrogen and phosphorus enrichment, 8-12 July 1979. Samples were from uplake (A) and downlake (D) stations in Lake Texoma.



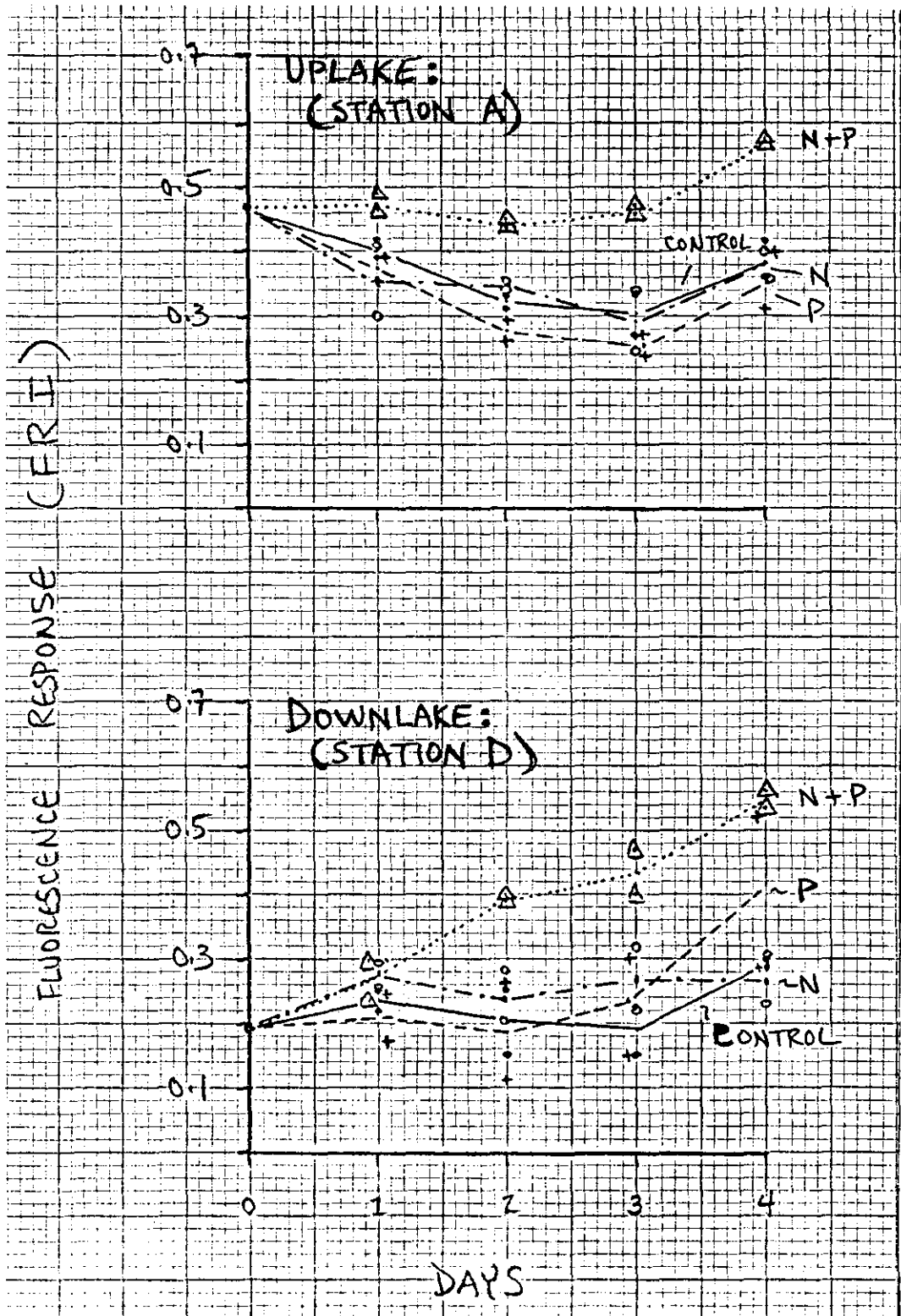


Figure 11. Response of phytoplankton photochemical capacity (as reflected by FRI) to experimental nitrogen and phosphorus enrichment of samples from uplake (A) and downlake (D) stations in Lake Texoma. The nutrient enrichment bioassay experiment was conducted 8-12 July 1979.

five watershed runoff enrichment experiments at the experimental pond facility of the USDA Southern Plains Watershed and Water Quality Laboratory. These experiments involved the addition of a simulated turbid watershed runoff mixture (a suspension of either San Saba clay or Bowie loam) to replicated water columns isolated by transparent polyethylene film. Control water columns received no runoff enrichment. The chlorophyll content of enriched and control water columns was determined just prior to the experimental runoff addition and for several days thereafter. San Saba clay was added as a component of the simulated watershed runoff on three occasions (experiments SS-1, SS-2 and SS-3), and Bowie loam on two occasions (BL-1 and BL-2). Characteristics of these soils and the nutrient content of the runoff mixtures are presented in Table 3.

Monitoring of water column suspended sediment content and sediment trap collections by O.R. Lehman revealed that the initial settling rate of Bowie loam is ca. 10x that of San Saba clay (Fig. 12). This large difference in sedimentation rate can be explained by the high sand content of Bowie loam and the high clay content of San Saba clay (Table 3). After the first day, the two soils settle out at about the same rate (ca.  $100 \text{ mg l}^{-1} \text{ day}^{-1}$ ). Significantly, the sedimentation rate of San Saba clay increased slightly after the initial day, probably due to flocculation of clay micelles resulting in aggregate formation and accelerated particle sinking rates. However, because of its lower initial sedimentation rate, San Saba clay consistently remained in the water column longer and produced higher turbidity levels than did Bowie loam.

Results of simulated watershed runoff experiments are presented in Fig. 13. In all cases, runoff addition resulted in an initial decrease in water column chlorophyll content which exceeded that in control tubes. Sedimentation

Table 3. San Saba clay and Bowie loam soil characteristics, and nutrient content of simulated watershed runoff mixtures added to experimental water columns.

	<u>Bowie Loam</u>	<u>San Saba Clay</u>
<u>Soil Characteristics:</u>		
% Sand	45	18
% Silt	40	33
% Clay	15	49
% Carbonates (as CaCO <sub>3</sub> )	0.06	3.2
pH	6.5	7.1
<u>Nutrient Content of Simulated Watershed Runoff (mg l<sup>-1</sup>)*:</u>		
Total P	1.70	1.20
Total Soluble P	0.02	0.37
Soluble Reactive P	0.01	0.26
Total Kjeldahl N	9.52	6.44
NO <sub>2</sub> <sup>-</sup>	0.02	0.44
NO <sub>3</sub> <sup>-</sup>	1.57	0.98
NH <sub>4</sub> <sup>+</sup>	0.33	1.45

\* Experimental runoff additions comprised 10% of the total experimental water column volume, thus nutrient additions to the water columns were approximately 0.1 of the above figures.

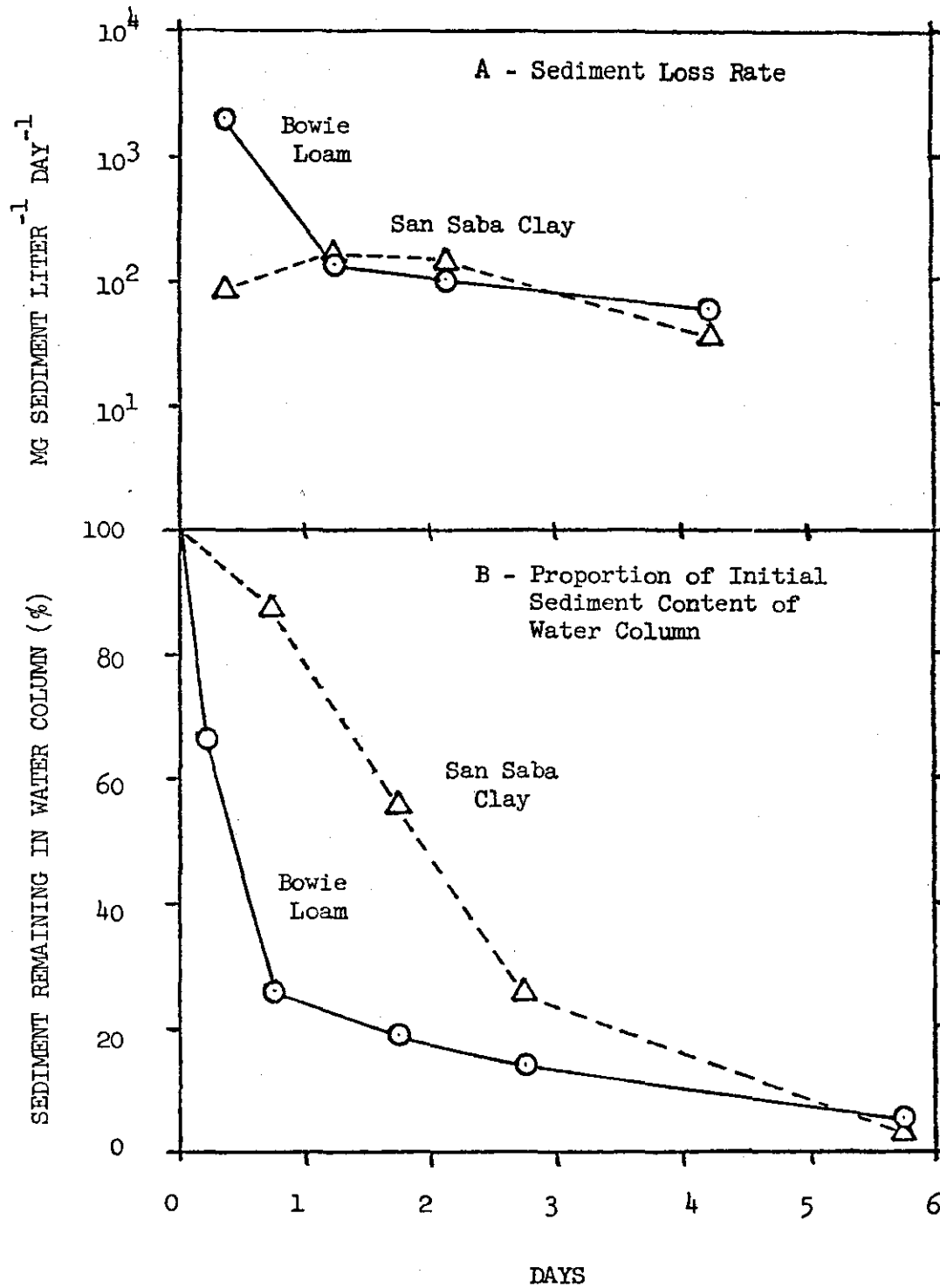


Figure 12. Comparison of Bowie loam and San Saba clay sedimentation rates (panel A) and relative rates of disappearance from the water column (panel B) during simulated watershed runoff experiments.

SAN SABA CLAY

BOWIE LOAM

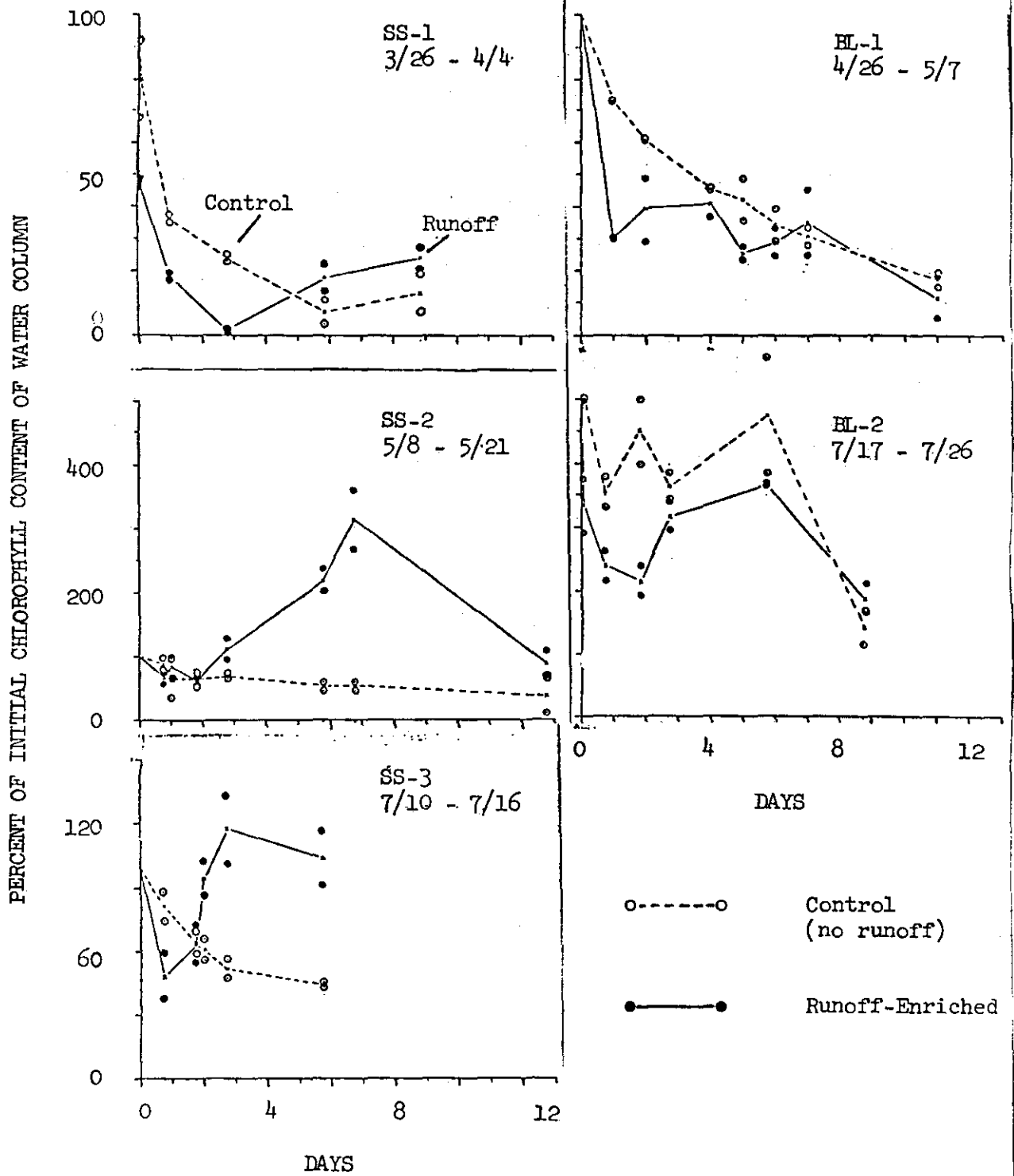


Figure 13. Effects of simulated watershed runoff on the chlorophyll content of experimentally isolated water columns. San Saba clay runoff experiments (SS-1, SS-2, SS-3) are on the left; Bowie loam runoff experiments (BL-1, BL-2) are on the right. These experiments were conducted in 1979 by O.R. Lehman.

trap collections demonstrated that runoff addition results in the downward displacement and physical removal of algal chlorophyll from the water column (O.R. Lehman, unpublished data). Although the mechanism of this removal remains uncertain, we hypothesize that coflocculation of phytoplankton cells by settling clay particle aggregates may be at least partially responsible.

Chlorophyll levels in Bowie loam runoff treatments (BL-1, BL-2) did not recover with time, but remained approximately equal to or less than controls. In contrast, San Saba clay runoff treatments (SS-1, SS-2, SS-3) stimulated algal biomass production after the initial decline in water column chlorophyll. Recovery and increase of algal chlorophyll was most evident in experiments SS-2 and SS-3. Cold, cloudy conditions after the second day of experiment SS-1 likely suppressed much of the algal biomass increase which may have occurred otherwise.

During the first two days of experiment SS-1, additional measurements were conducted to determine the effects of turbid, but nutrient-rich, watershed inflow on (i) phytoplankton photosynthesis rates, (ii) the photochemical capacity of algal assemblages, and (iii) the size distribution of planktonic microheterotrophic activity (primarily bacterial) activity in receiving waters. Samples taken from 0.5 m in control (no runoff added) and experimental (runoff-enriched) water columns were inoculated with tracer quantities of <sup>14</sup>C-labelled sodium acetate, incubated in situ, and then size-fractionated by gentle vacuum filtration of small (10-20 ml) subsamples through a series of Nucleopore filters and Nytex screens. Runoff addition resulted in a dramatic shift in the size distribution of microheterotrophic activity toward larger particle sizes (Fig. 14). In control samples only

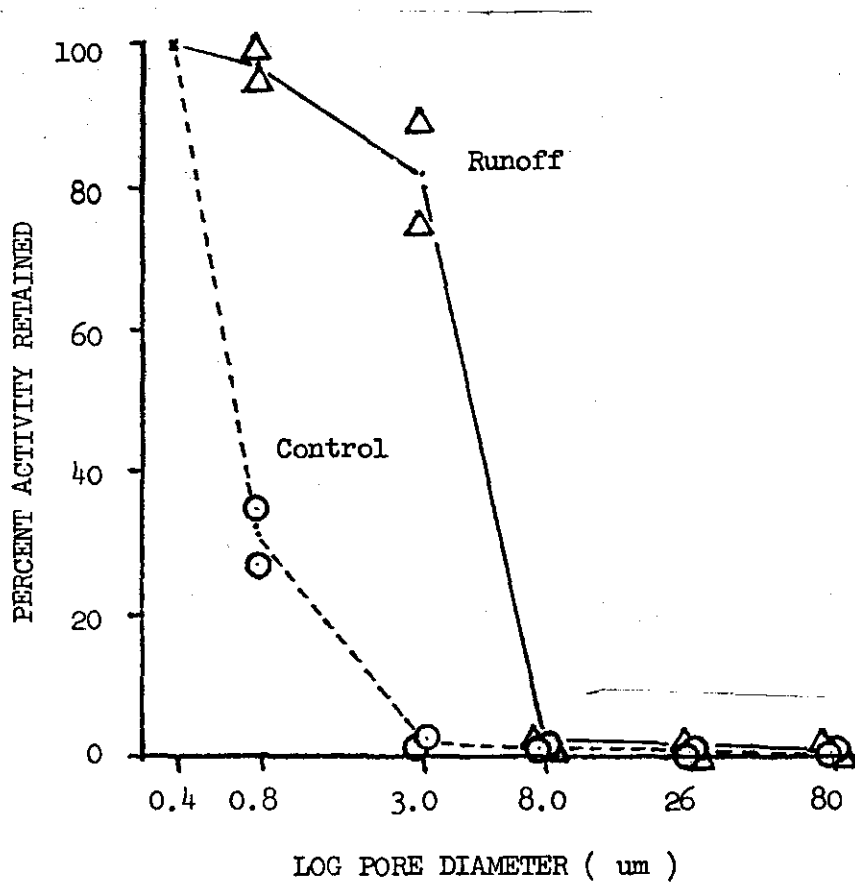


Figure 14. Size distribution of microheterotrophic activity (as reflected by dark uptake of  $^{14}\text{C}$ -labelled sodium acetate) in a San Saba clay runoff-enriched water column (Runoff) and an unenriched (Control) water column. Samples taken during experiment SS-1 from 0.5 m.



about 30% of total acetate uptake was associated with particles  $> 0.8 \mu\text{m}$ , thus indicating that at least 70% was associated with free-living, rather than attached, bacteria. Only 2% of the total microheterotrophic activity was associated with particles  $> 3 \mu\text{m}$ . In contrast, 95% of total microheterotrophy in the runoff-enriched water column was associated with  $> 0.8 \mu\text{m}$  particles (i.e., only 5% unattached) and 80% with 3 - 8  $\mu\text{m}$  particles. Very little ( $< 2\%$ ) of the total activity occurred in the  $> 8 \mu\text{m}$  fractions in either control or experimental systems. Although the results clearly show that formerly free-living bacteria were associated with larger particles in the runoff-enriched system, whether they (i) actively attach to, (ii) passively adsorb to, or (iii) are coflocculated by introduced clay particles remains undetermined.

Control and experimental water columns were also compared in regard to algal photosynthesis rates (as reflected by  $\text{NaH}^{14}\text{CO}_3$  uptake) and algal physiological status (as reflected by FRI, see section 4.1). Results of these comparisons are summarized in Table 4. Simulated watershed runoff stopped photosynthetic production by phytoplankton in the experimental tube. Exchange of  $^{14}\text{C}$  uptake samples (i.e., samples from the control tube incubated in the experimental tube, and vice-versa) on the second day of the experiment demonstrated that the reduction in photosynthesis was due to the unavailability of light in water columns receiving runoff. Photosynthesis rates were reduced by 95% in control samples incubated at 0.5 m in the experimental tube. Samples from the experimental tube incubated in a control water column showed increased carbon uptake rates; however, photosynthesis was only 15% ( $1.10 \div 7.38 = 0.15$ ) of that in control samples, probably due to reduced algal biomass in the experimental tube. This experimental result corresponds well with the algal chlorophyll recovery with time evident in SS-1, SS-2 and

Table 4. Results of experiments conducted during SSC-1 to determine the physiological effects of watershed runoff on phytoplankton communities. C denotes samples from unenriched control water columns; E = samples from runoff-enriched water columns; C→E and E→C indicate experimental displacement of samples for incubation.

	<u>Treatment</u>	<u>Day 1</u>	<u>Day 2</u>
ALGAL BIOMASS:			
mg Chl a m <sup>-3</sup>	C	14.8	5.5
	E	18.1	3.1
F <sub>d</sub> (in cps)	C	554	485
	E	853	343
ALGAL PHOTOSYNTHESIS AND PHOTOSYNTHETIC CAPACITY:			
mg C m <sup>-3</sup> hr <sup>-1</sup>	C	9.46	7.38
	C→E	-	0.38
	E	0	0.05
	E→C	-	1.10
mg C / mg Chl a / m <sup>-3</sup> hr <sup>-1</sup> lt <sup>-1</sup>	C	-	1.34
	E	-	0.35
Photochemical Capacity (FRI)	C	0.52	0.51
	E	0.39	0.30

SS-3 (Fig. 13), and together, these data suggest that while turbid inflow can reduce or stop photosynthesis by limiting light penetration, algal production and biomass recovery occurs as soon as light is no longer limiting. Subsequent stimulation of algal productivity will depend upon the degree of nutrient limitation of the phytoplankton assemblage and whether or not the nutrient content of the water column is supplemented significantly by the runoff influx.

Biomass-specific photosynthesis rates (i.e., mg C fixed / mg Chl a m<sup>-3</sup>) and in vivo chlorophyll fluorescence response to DCMU (i.e., FRI) indicate a depression of algal photochemical capacity in the experimental tube (Table 4). The physiological condition of phytoplankton not removed from the water column, therefore, appears to be reduced by light deprivation, as previously indicated in laboratory light deprivation experiments (Section 4.1, Fig. 3).

In summary, measurements of microheterotrophic activity, extracted chlorophyll, in vivo chlorophyll fluorescence and phytoplankton photosynthesis made in conjunction with experiment SS-1 indicate the following:

- 1) Bacteria become associated with suspended particles introduced by watershed runoff, but the mechanism of this association remains unclear at present. Coflocculation of bacterial cells by clay particle aggregates, rather than active bacterial attachment to suspended particles, is hypothesized.
- 2) Runoff appears to cause displacement of algal cells from the water column by some physical mechanism, again possible via coflocculation with clay particles.
- 3) Turbidity associated with simulated watershed runoff initially reduces photosynthesis by decreasing light penetration into the water column.
- 4) Runoff depresses the physiological condition of algal cells remaining

in the water column, likely due to effects of light deprivation.

5) Algae appear capable of rapid recovery when light availability increases, and algal production within the euphotic zone may be stimulated by increased nutrient availability.

#### Lake Texoma Watershed Runoff Experiment

An additional watershed runoff experiment was conducted in situ in Lake Texoma during July 1980. Three transparent polyethylene-film cylinders (Section 3.5) were constructed and installed in the boat harbor of the University of Oklahoma Biological Station. The experimentally-isolated water columns were left unperturbed for six days to permit an equilibrium to be established. Simulated runoff mixtures of Lake Texoma water and either San Saba clay or Bowie loam were made (runoff soil concentration =  $50 \text{ g l}^{-1}$ ), and carefully added to the surface layer of the appropriate experimental water column. A third water column received no runoff addition and served as a control.

Initial phytoplankton photosynthesis rate measurements were made on July 5. The simulated runoff mixtures were added at 1100 on July 6, and individual series of physical-chemical measurements were made at 1000 and 1200. Carbon uptake samples were obtained just prior to runoff addition, and incubated in situ just after runoff addition in order to determine effects on phytoplankton productivity due solely to reduced light penetration. Subsequent productivity measurements were made on 7, 8 and 10 July.

Experimental results are summarized in Figs. 15 and 16. The magnitude and vertical distribution of algal productivity remained near constant in the control water column. Photosynthetic carbon uptake was reduced at all depths by San Saba clay runoff, but was relatively unaffected by Bowie loam runoff (Fig. 15). The anomalously low surface productivity value in the Bowie loam

PHYTOPLANKTON PHOTOSYNTHESIS (  $\text{mg C m}^{-3} \text{ hr}^{-1}$  )

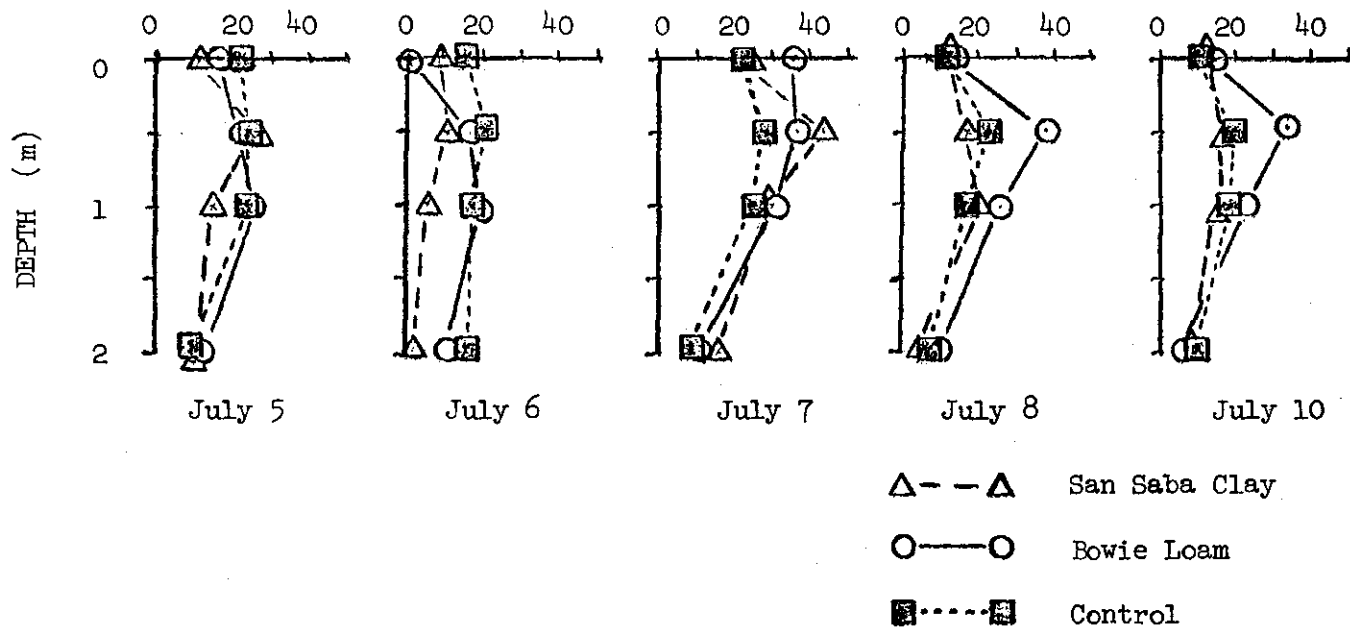


Figure 15. Vertical distribution of phytoplankton photosynthesis in experimental and control water columns during in situ watershed runoff experiments in Lake Texoma, 5-10 July 1980.

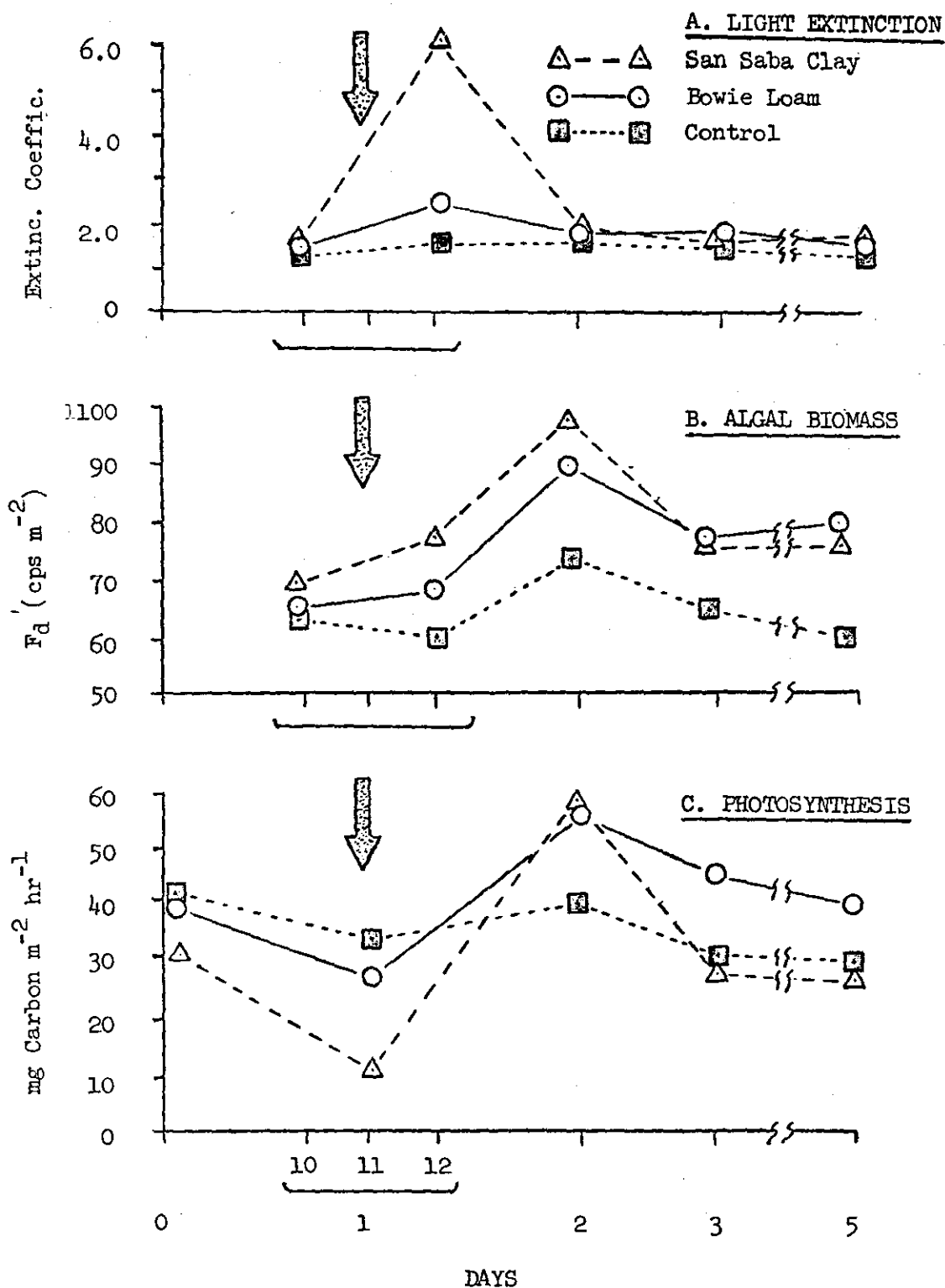


Figure 16. Comparison of light extinction, algal biomass and integral phytoplankton productivity in San Saba clay runoff, Bowie loam runoff and control water columns; Lake Texoma, 5-10 July 1980. The arrow indicates the time of runoff addition.

enriched water column is likely due to severe photoinhibition of the sample (probably due to methodological error).

San Saba clay runoff addition resulted in much higher light extinction and more persistent turbidity than did Bowie loam runoff (Fig. 16). However, with addition of lower suspended sediment concentrations than used in the 1979 experiments, high turbidity persisted only one day and both San Saba clay and Bowie loam runoff enriched water columns responded quickly with increased phytoplankton productivity and biomass. By 8 and 10 July, photosynthesis rates in the San Saba clay water column returned to control levels, while that in the Bowie loam water column remained slightly higher (Fig. 16). Unlike the 1979 pond experiments, marked vertical displacement of phytoplankton biomass (as reflected by  $F_d$ ) concurrent with runoff particle settling did not occur, thus suggesting that particle concentration thresholds probably exist for algal cell - clay particle coflocculation.

#### Soil-Nutrient Enrichment Bioassay Experiments

Plant nutrients are associated with both the dissolved and particulate phases of natural watershed runoff. Soil-nutrient enrichment bioassay experiments with Lake Texoma phytoplankton assemblages were conducted in an effort to distinguish (i) the roles of dissolved and particle-associated nutrients and (ii) the role of particle surface effects in influencing phytoplankton productivity and the size distributions of autotrophic and microheterotrophic activities. Methods employed in these experiments and treatment codes are described in Section 3.3.

Experimental results are summarized in Figs. 17 and 18. Phytoplankton photochemical capacity was high ( $FRI = 0.5-0.6$ ) at the initiation of the experiment and did not fluctuate greatly in the experimental systems (Fig. 17),

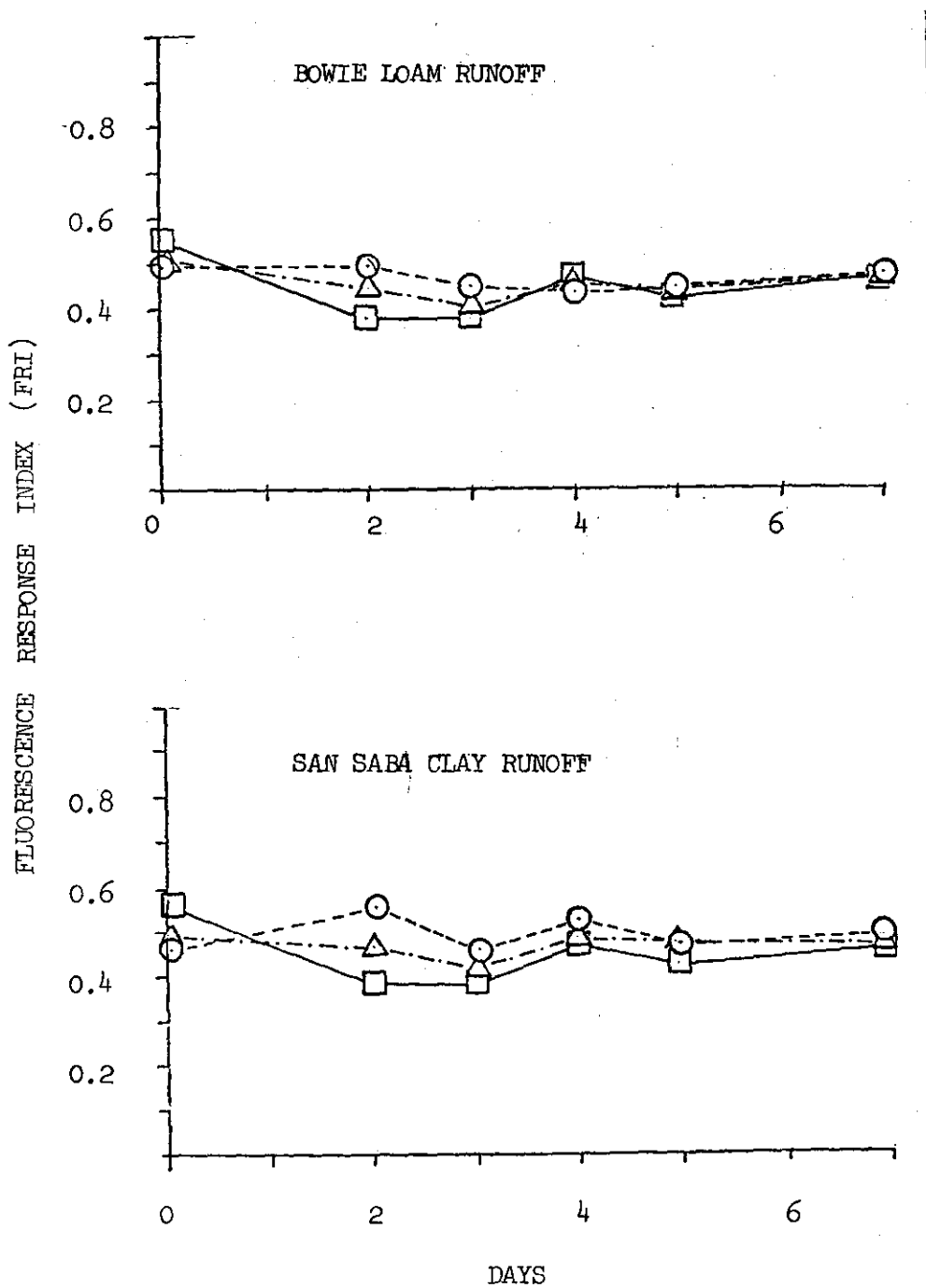


Figure 17. Response of Lake Texoma phytoplankton photochemical capacity (as reflected by FRI) in soil-nutrient enrichment bioassay experiments, 14-21 July 1980. Circles = soil particles + leached nutrients, triangles = leached nutrients only, squares = unenriched controls. Each point represents the mean of duplicates.



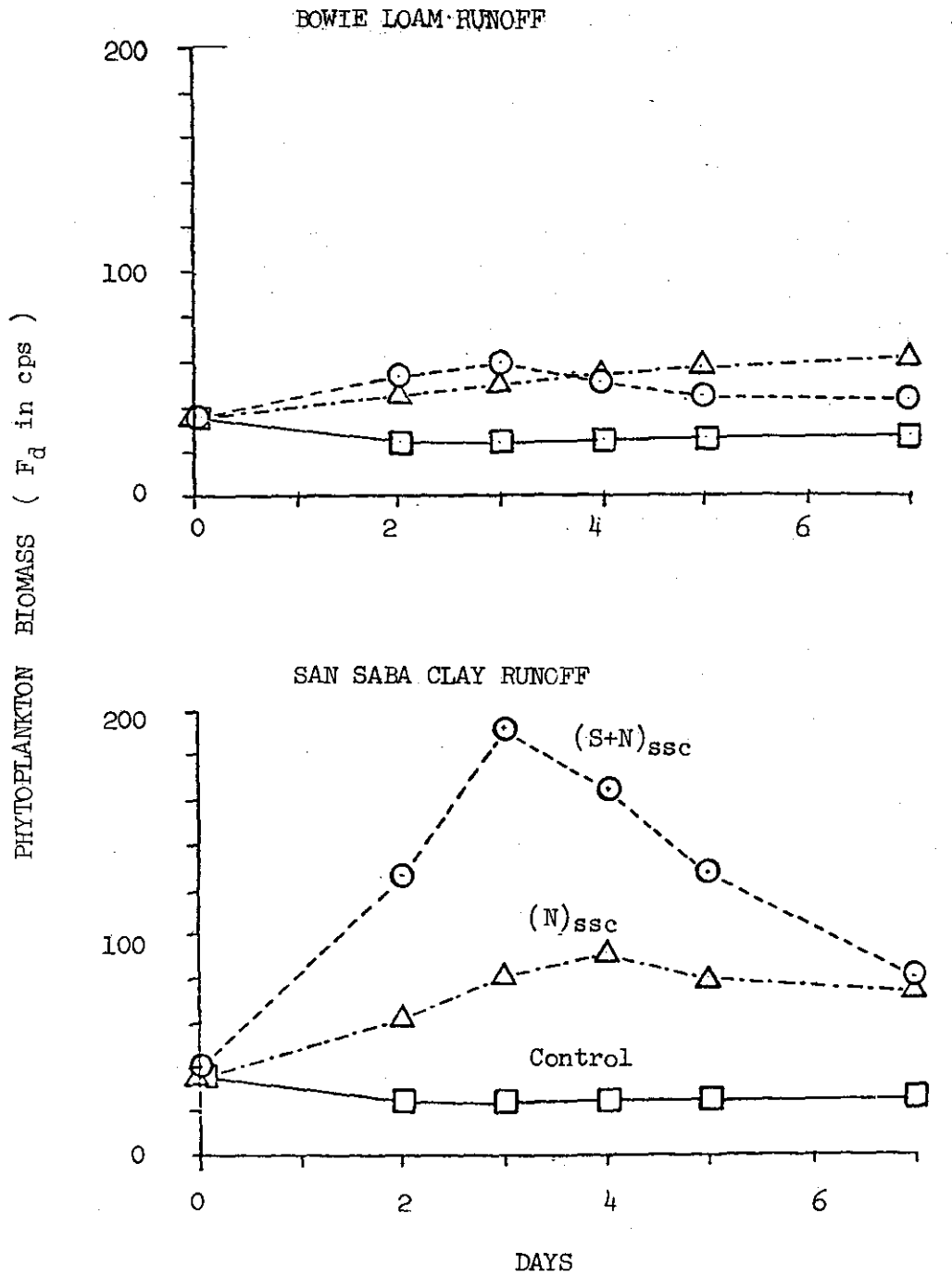


Figure 18. Response of Lake Texoma phytoplankton biomass (as reflected by  $F_d$ ) in soil-nutrient enrichment bioassay experiments, 14-21 July 1980. Circles = soil particles + leached nutrients, triangles = leached nutrients only, squares = unenriched controls. Each point represents the mean of duplicates.

although the control FRI declined slightly (to 0.4). Algal biomass (as reflected by  $F_d$ ) did not change significantly in Bowie loam systems, but increased about 2-fold in the  $(N)_{SSC}$  treatment and 5-fold in the  $(S+N)_{SSC}$  treatment (Fig. 18). These data indicate that nutrient desorption from San Saba clay is considerably greater than that from Bowie loam, and that further desorption from San Saba clay particles occurred during the experimental period.

Effects on size distributions of autotrophy and microheterotrophy during the experimental period were not easily interpreted. Size distribution of autotrophic  $^{14}C$  uptake did not change greatly in controls or in nutrient-only systems (i.e.,  $(N)_{SSC}$  and  $(N)_{BL}$ ). The proportion of larger cells increased in  $(S+N)_{SSC}$ , but decreased in  $(S+N)_{BL}$  in correspondence with the higher nutrient content of, and nutrient desorption from, San Saba clay relative to Bowie loam. Microheterotrophy associated with larger particles ( $> 3, > 8$ ) increased in controls, decreased slightly in  $(S+N)_{SSC}$ , and remained about the same in  $(S+N)_{BL}$ ,  $(N)_{BL}$  and  $(N)_{SSC}$  treatments. In general, a shift occurred toward larger algae and smaller bacteria in the higher nutrient conditions (i.e., in association with SSC systems), with the presence of particles not being of major influence.

Except for photosynthetic  $^{14}C$  uptake in  $(S+N)_{SSC}$  and  $(N)_{SSC}$  systems, all net autotrophic and microheterotrophic activities declined from their initial levels (Fig. 19). These results demonstrate a significant stimulation of phytoplankton productivity upon introduction of nutrients associated with watershed runoff, whether in dissolved or particle-associated phases.

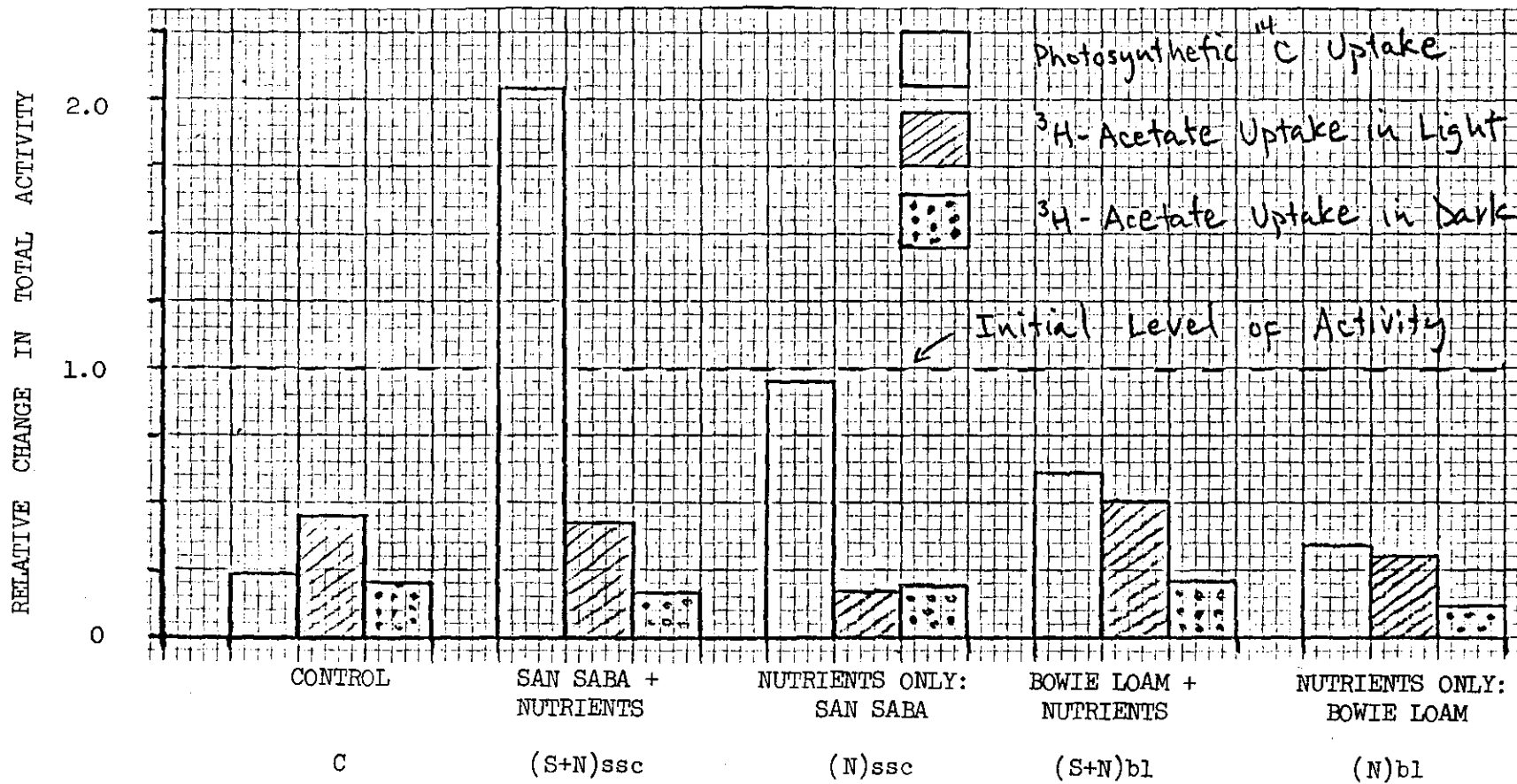


Figure 19. Relative change in microbial autotrophic and microheterotrophic activities in 1-week soil-nutrient enrichment bioassays, 14-21 July 1980.

#### 4.3. In Situ Effects of Turbid Watershed Inflow to Lake Texoma

We observed in situ effects of turbid watershed inflow on water column physical-chemical characteristics and biological productivity in Lake Texoma during the springs of 1978, 1979 and 1980.

In 1978, measurements of chlorophyll fluorescence and microbial adenosine triphosphate (ATP) concentrations were made along transects intersecting an advancing surface turbidity plume (Fig. 20) in order to determine if (i) watershed runoff directly enriches lake water with terrigenous and river-derived microorganisms (e.g., algae, free-living and attached bacteria), or (ii) watershed inflow results in a dilution of lake water microbiota. Transect samples obtained on June 12 are compared in regard to microbial ATP, relative turbidity and chlorophyll fluorescence ( $F_d$ , FRI) in Table 5. Water transparency (as reflected by Secchi depth) was positively correlated with ATP and chlorophyll levels (Fig. 21), indicating alternative (ii) above. Although watershed inflow is far from sterile, and undoubtedly contains terrigenous and river-derived microorganisms, the "newer" inflowing water is initially less fertile microbially than the "older" resident lake water.

In 1979, a series of fluorescence vertical profiles were obtained at two Lake Texoma stations (B and C, Fig. 1) prior to and during the occurrence of a major watershed inflow event. A surface turbidity plume progressed through station B and the Secchi depth decreased from 1.25 m on June 11 to 0.3 m on June 12 (Fig. 22). Conductance profiles at station B showed the inflowing water to be confined to a 2-m thick surface layer on June 12 and to have become an 8-m thick layer by June 13 (Fig. 23). Although turbidity at station C increased gradually from June 8 - 13, there were no major fluctuations in conductance.

Chlorophyll fluorescence profiles at station B indicate significant

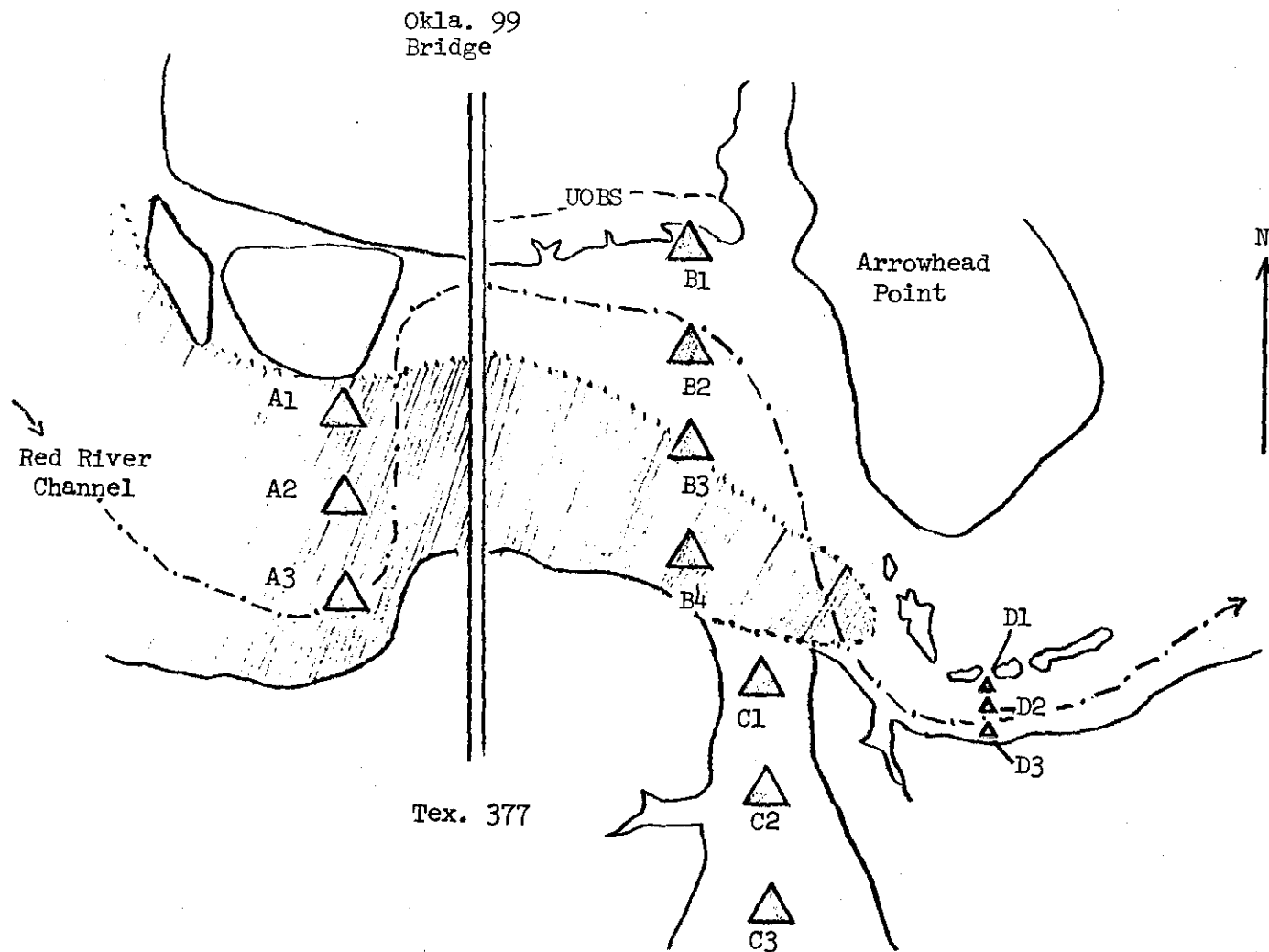


Figure 20. Map of the Red River arm of Lake Texoma in the vicinity of the Willis (OK 99-TX 377) Bridge and the University of Oklahoma Biological Station (UOBS). Triangles denote the location of sampling stations in transects across an advancing turbidity plume, 12 June 1978. The cross-hatched area indicates the approximate location of the turbidity plume at the time of sampling.

Table 5. Phytoplankton biomass ( $F_d$ ), photochemical capacity (FRI) and microbial carbon (determined by ATP analysis) along transects across a turbidity plume in the Red River arm of Lake Texoma, 12 June 1978. All samples from 1-m depth.

---

<u>Sample</u>	<u>Secchi Depth (m)</u>	<u><math>F_d</math> (cps)</u>	<u>FRI</u>	<u>Microbial C (<math>\mu\text{g l}^{-1}</math>)</u>
A1	0.50	114	0.48	133
A2	0.40	121	0.48	133
A3	0.40	118	0.50	149
B1	0.75	222	0.58	629
B2	0.70	219	0.55	341
B3	0.60	214	0.56	308
B4	0.50	201	0.58	231
C1	0.75	192	0.57	269
C2	0.75	225	0.59	322
C3	0.80	182	0.56	263
D1	0.85	339	0.59	280
D2	0.75	246	0.58	263
D3	0.80	190	0.58	229

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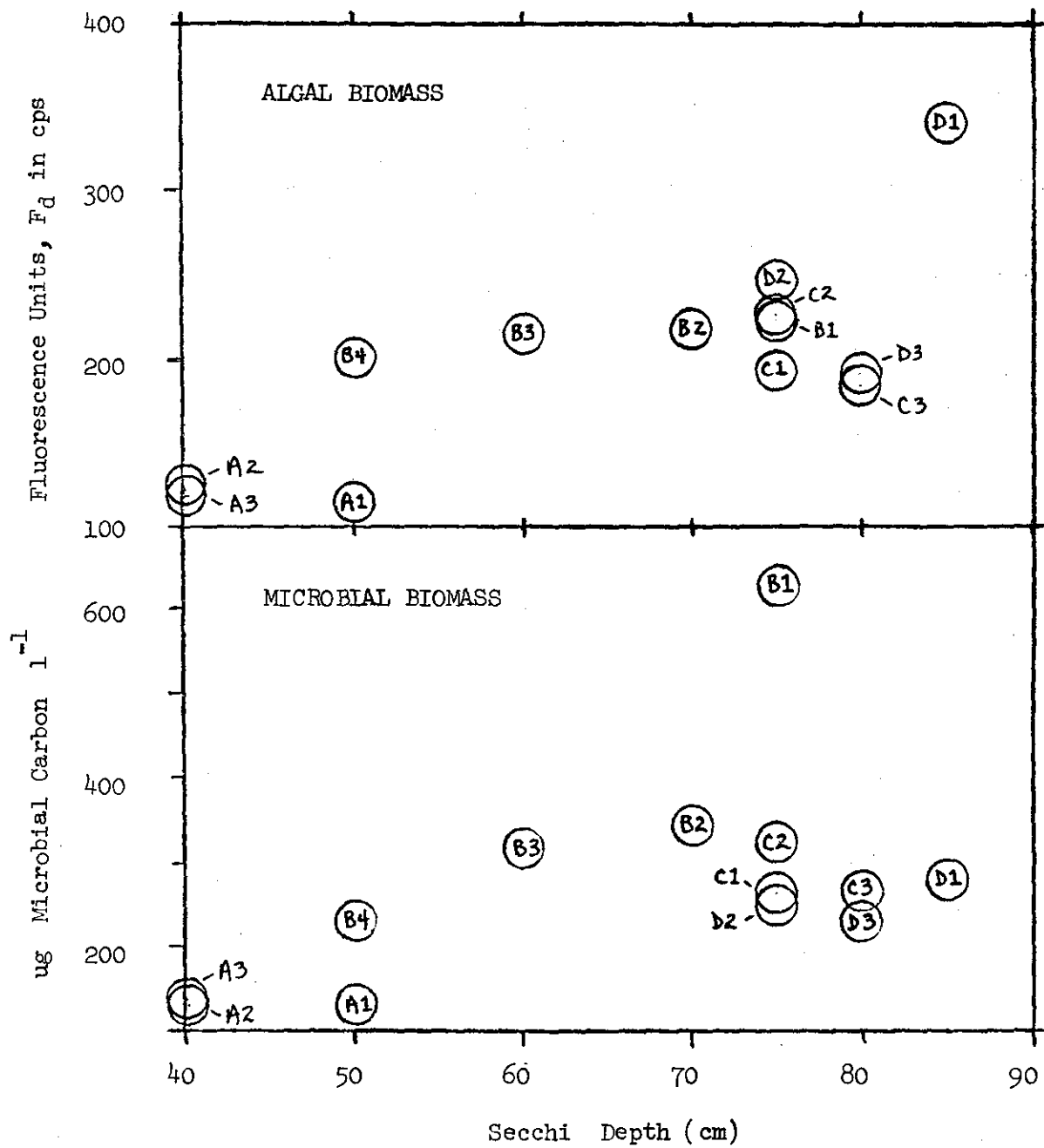


Figure 21. Effect of watershed inflow on algal and microbial biomass in the Red River arm of Lake Texoma, 12 June 1978. Stations A1, A2, A3 and B4 were within the turbidity plume. See Fig. 20 for station locations.

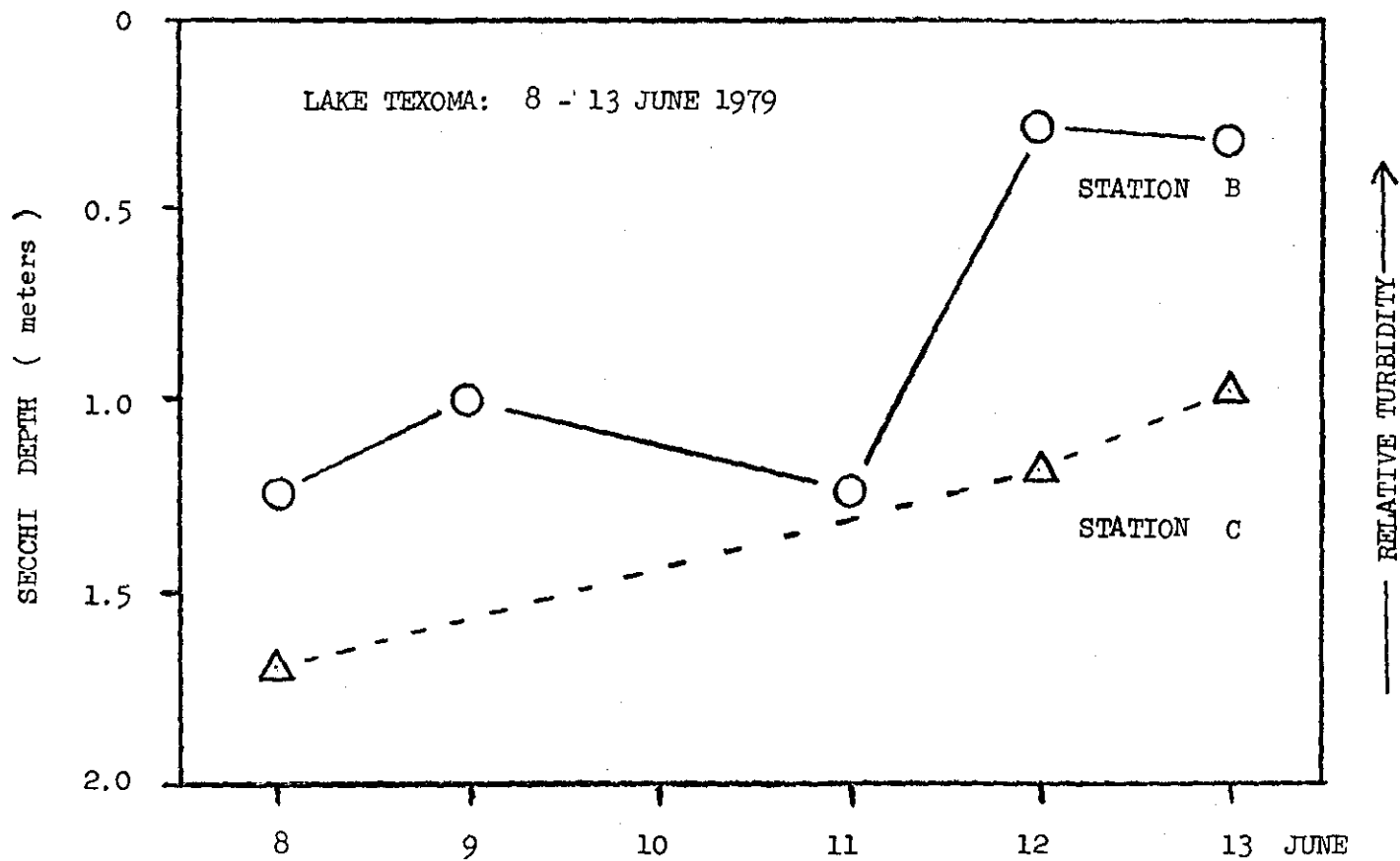


Figure 22. Changes in relative turbidity (as reflected by Secchi depth) at Lake Texoma stations B (UOBS) and C (channel) during the 8-13 June 1979 watershed inflow event.



STATION B:

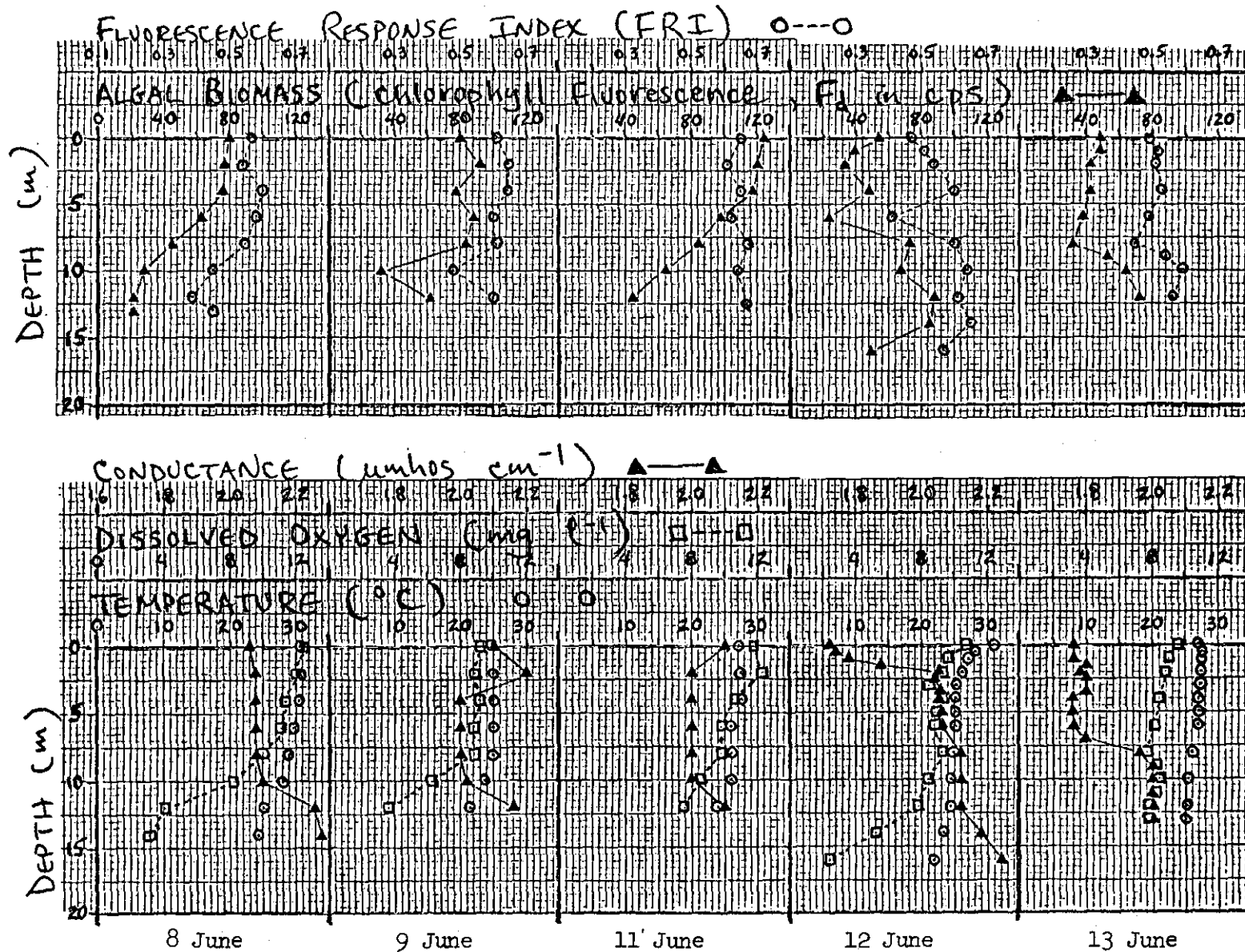


Figure 23. Vertical profiles of phytoplankton photochemical capacity (FRI), phytoplankton biomass ( $F_d$ ), conductance, dissolved oxygen and water temperature at station B (UOBS) during the 8-13 June 1979 watershed inflow to Lake Texoma.

shifts in the vertical distribution of phytoplankton biomass and physiological photochemical capacity (as reflected by  $F_d$  and FRI, respectively), associated with the turbid watershed inflow (Fig. 23). Such changes may be explained by two mechanisms: (i) advective displacement of the upper portion of the water column by inflowing water, and (ii) vertical displacement of phytoplankton cells by co-flocculation with settling river-borne particles and a concurrent depression of FRI by light deprivation (as noted in the 1979 watershed runoff experiments, Section 4.2). Operation of mechanism (i) is evident from comparison of  $F_d$  and conductance profiles for station B on June 11, 12 and 13. Algal biomass in the upper 6 m of water column on June 11 (100-120  $F_d$  cps) was reduced by approximately 50% (to ca. 40  $F_d$  cps) by June 12. However, the June 12 conductance profile showed the inflowing water mass to be confined to a 2-m thick surface layer. Therefore, although the June 11-12 decline in phytoplankton biomass in the 2-m surface layer can be explained by advective displacement by phytoplankton-poor inflowing water, decreases at 4, 6 and 8 m, and increases at 12 m suggest the concurrent vertical displacement of phytoplankton cells.

Conductance,  $F_d$  and FRI profiles at station B on June 13 were parallel, and showed the inflowing water to extend to about 7 - 8 m. The discrete, 2-m thick surface plume of June 12 was dispersed and mixed within the UOBS basin by southerly winds before it progressed to station C. Station C profiles on June 12 and 13 (Fig. 24) indicate a parallel depression of algal biomass and conductance between 6 and 14 m, and suggest that the inflowing water mass proceeded downstream from the UOBS basin as an interflow.

A similar episode of watershed inflow to the Red River arm of Lake Texoma occurred during May 1980, and was intensively monitored at three

STATION C:

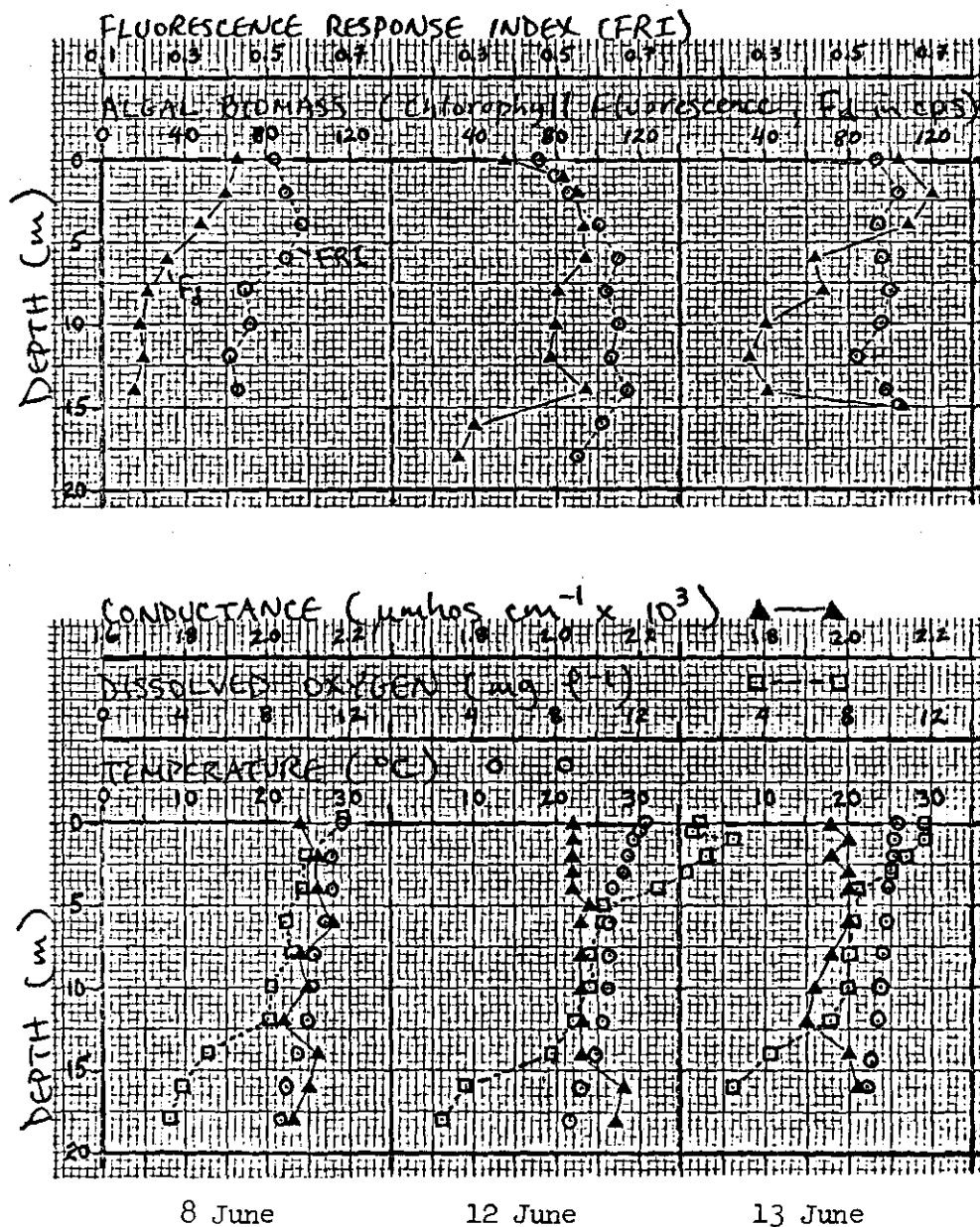


Figure 24. Vertical profiles of phytoplankton photochemical capacity (FRI), phytoplankton biomass ( $F_d$ ), conductance, dissolved oxygen and water temperature at station C (channel) during the 8-13 June 1979 watershed inflow to Lake Texoma.

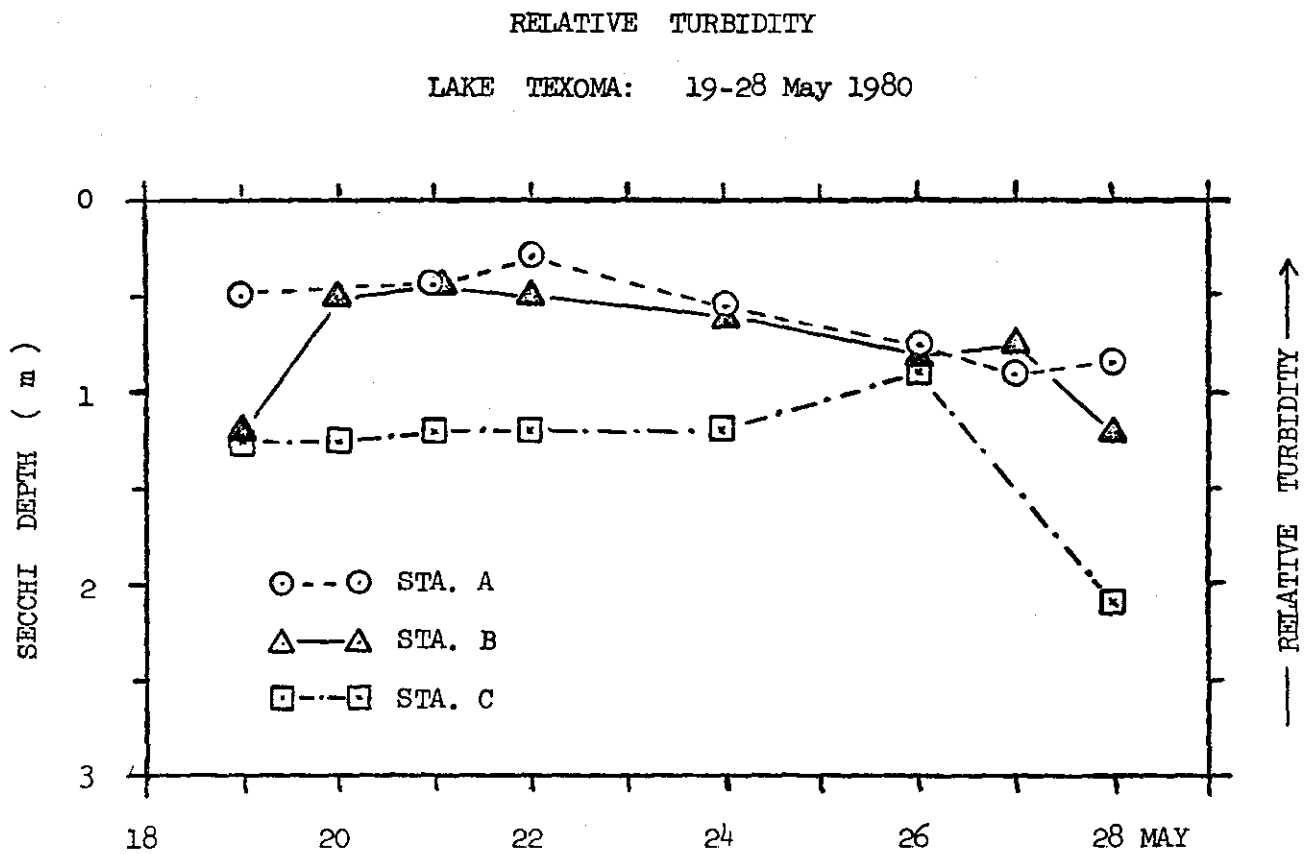


Figure 25. Changes in relative turbidity (as reflected by Secchi depth) at Lake Texoma stations A (uplake), B (UOBS) and C (channel) during the 18-28 May 1980 watershed inflow event.

stations (A, B and C, Fig. 1) over a 10-day period (May 19-28). The 1980 watershed inflow event was neither as turbid or as extensive as the June 1979 event described above. The inflowing turbid water mass reached the uppermost station (A) on May 18, and progressed to station B by May 20 (Fig. 25). As in June 1979, the turbidity plume was dispersed throughout the UOBS basin by southerly winds prior to progressing downstream through the narrow channel (station C) connecting the UOBS basin (station B) and the main reservoir basin (station D) of Lake Texoma. Turbidity did not increase at station C until May 26, and then to only one-half of that at stations A and B on May 21 (Secchi depth = 1.0 m at C, as compared to 0.5 m at A and B).

Fig. 26a-e shows vertical distributions of water temperature (a), dissolved oxygen (b), conductance (c), phytoplankton biomass (d) and photochemical capacity (e) at Lake Texoma stations A, B and C during May 19-28. Watershed inflow did not produce major physical-chemical effects except for increasing light extinction in near-surface layers. Phytoplankton biomass at station A declined initially (e.g., V-19 and V-22, Fig. 26d), but recovered rapidly as turbidity decreased (e.g., V-26 and V-28). Calm, sunny weather and decreasing turbidity at stations A and B resulted in marked solar heating of near-surface water (Fig. 26a) and pronounced phytoplankton biomass peaks within the euphotic layer (Fig. 26d). Although relative turbidity increased slightly at station C on May 26, it was equivalent to that already present at stations A and B (Secchi depth at all three stations = 1 m), and a similar near-surface peak in phytoplankton biomass occurred at station C.

The upper two panels of Fig. 27 compare phytoplankton photosynthesis rates, photochemical capacity and algal biomass at Lake Texoma stations

Figure 26 a-e. Vertical distribution of water temperature (a), dissolved oxygen (b), conductance (c), phytoplankton biomass (d) and phytoplankton photochemical capacity (e) at Lake Texoma stations A (uplake), B (UOBS) and C (channel) during the 18-28 May 1980 watershed inflow event.

Fig. 26 a.

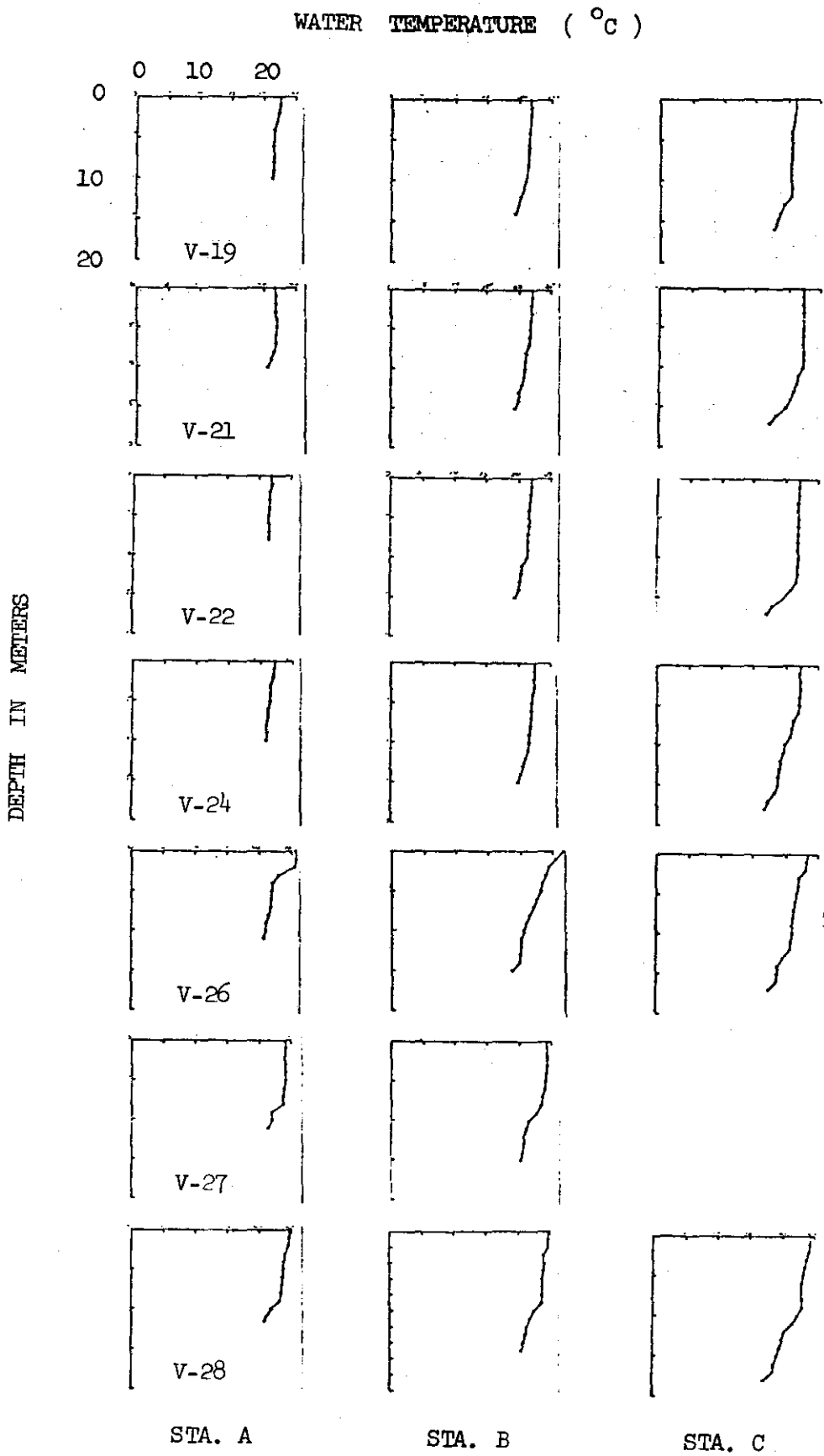


Fig. 26 b.

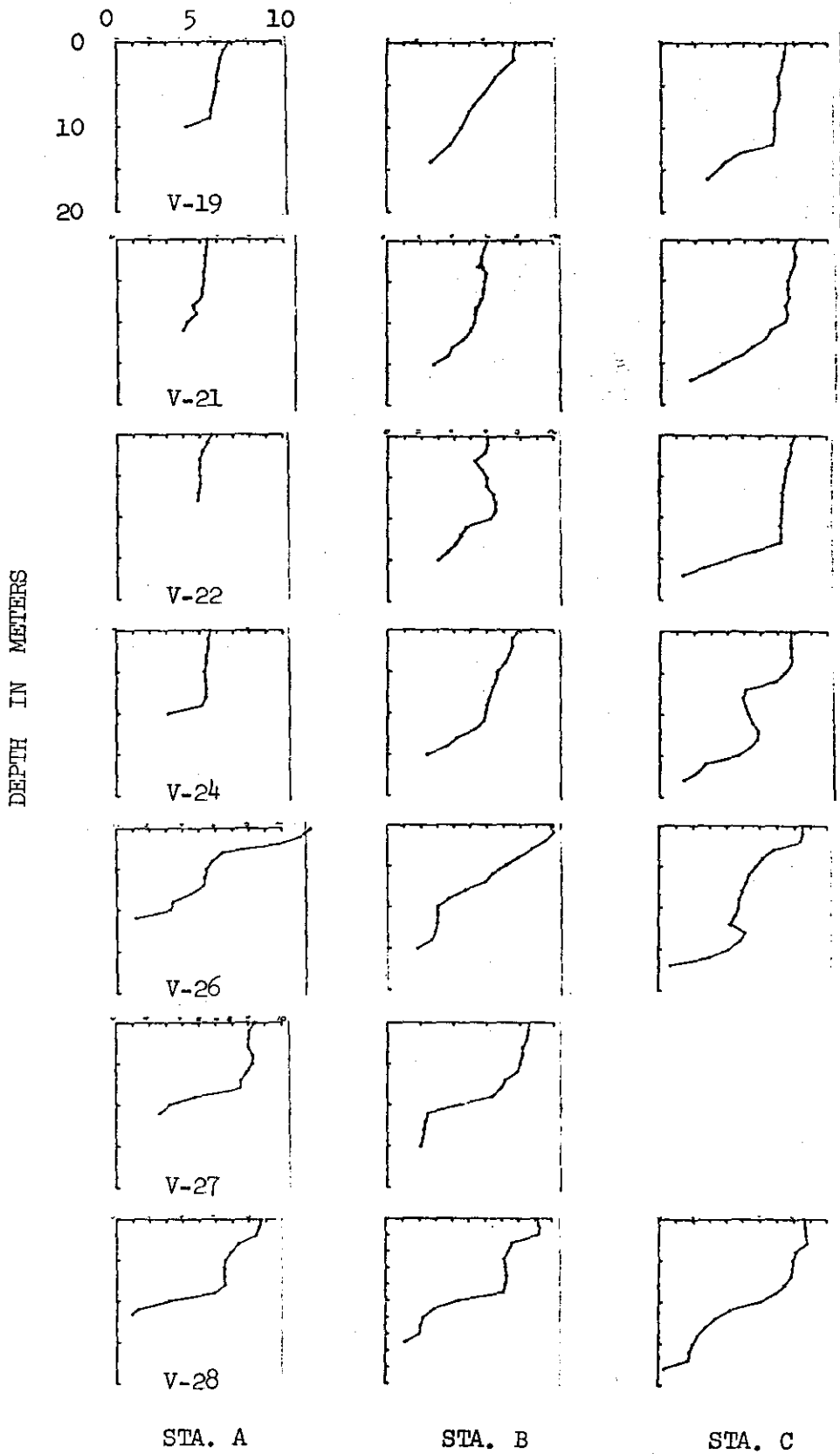
DISSOLVED OXYGEN ( mg liter<sup>-1</sup> )



Fig. 26 c.

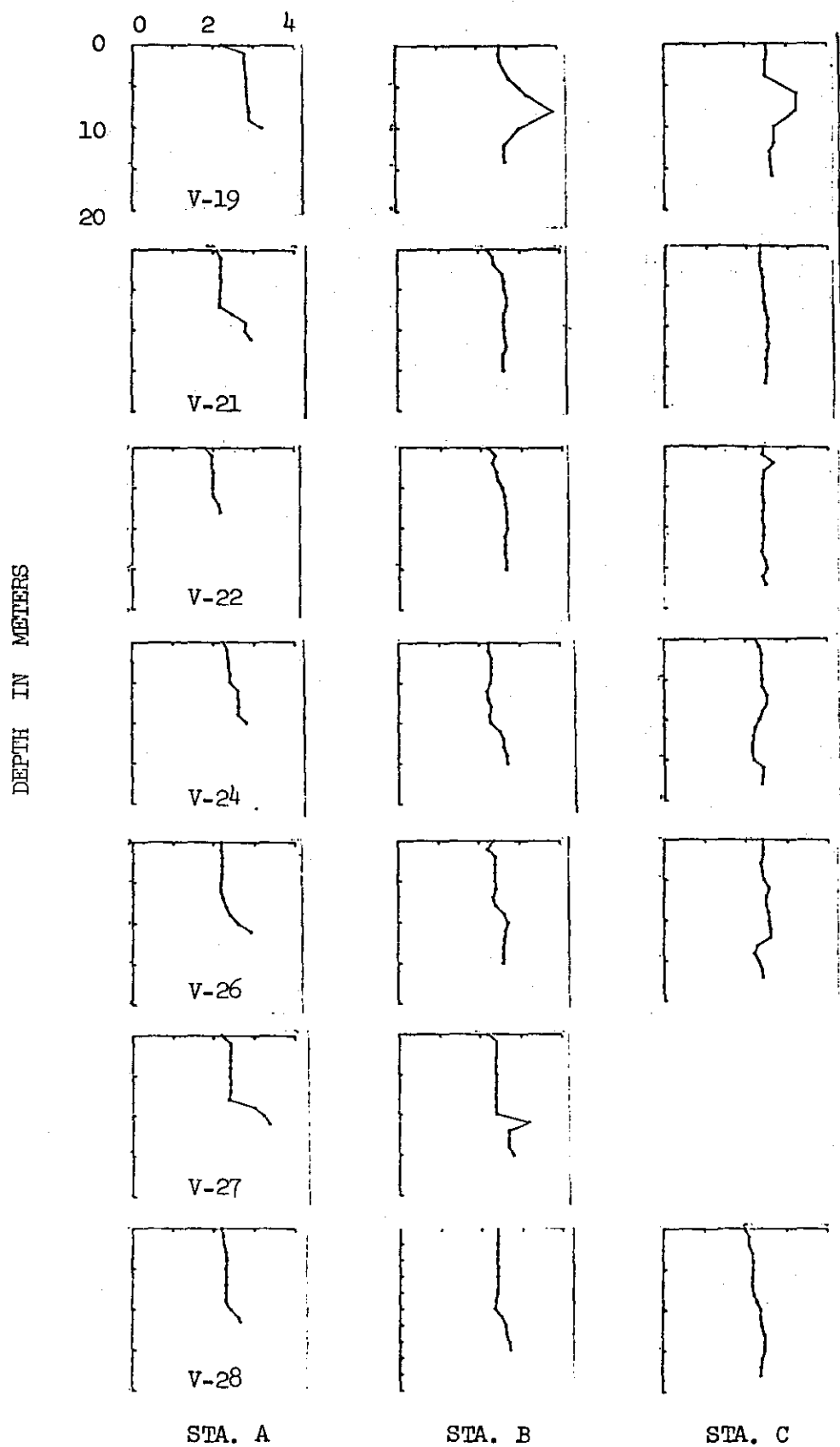
CONDUCTANCE (  $\mu\text{mhos cm}^{-1} \times 10^3$  )

Fig. 26 d.

## PHYTOPLANKTON BIOMASS

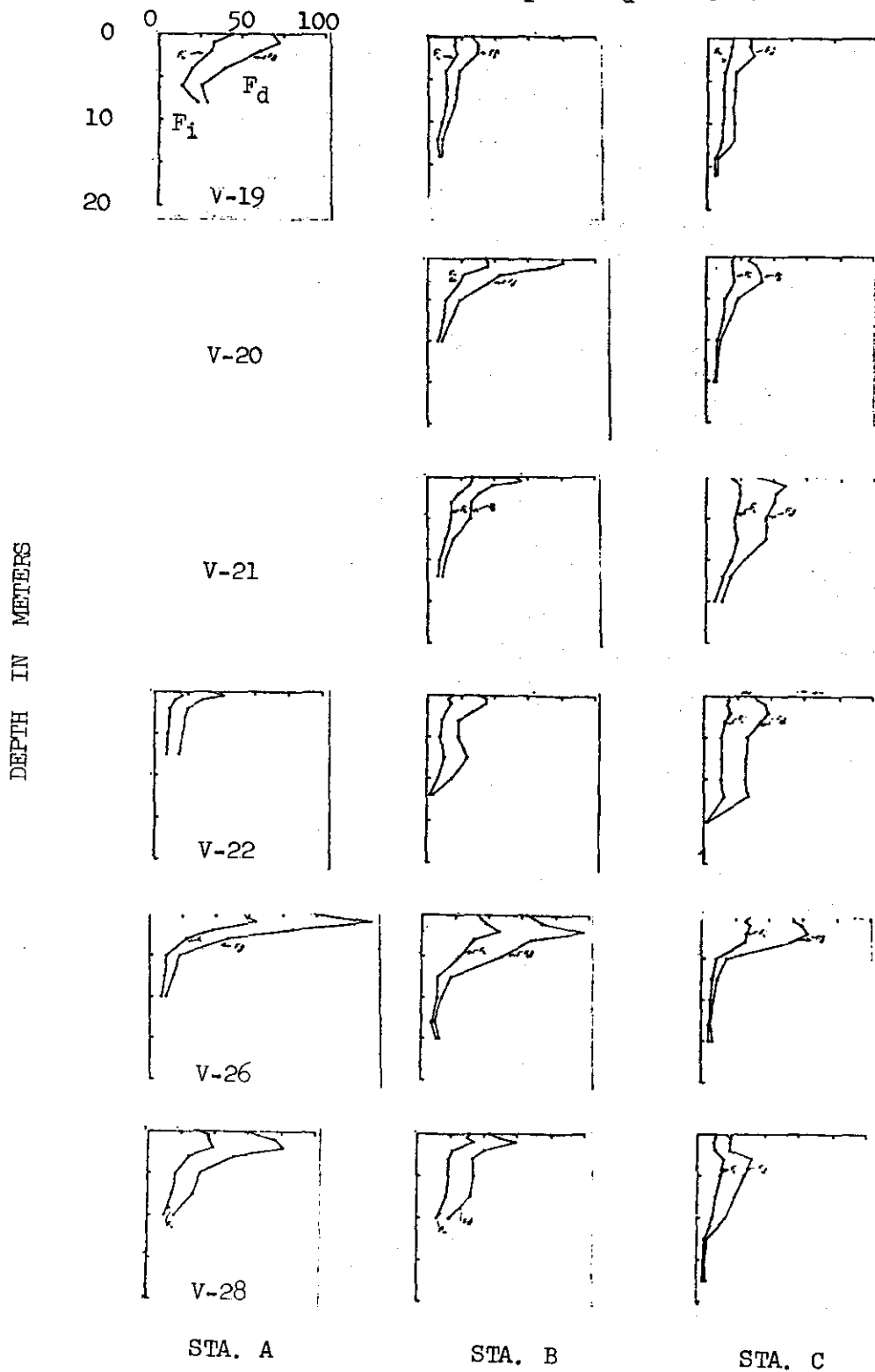
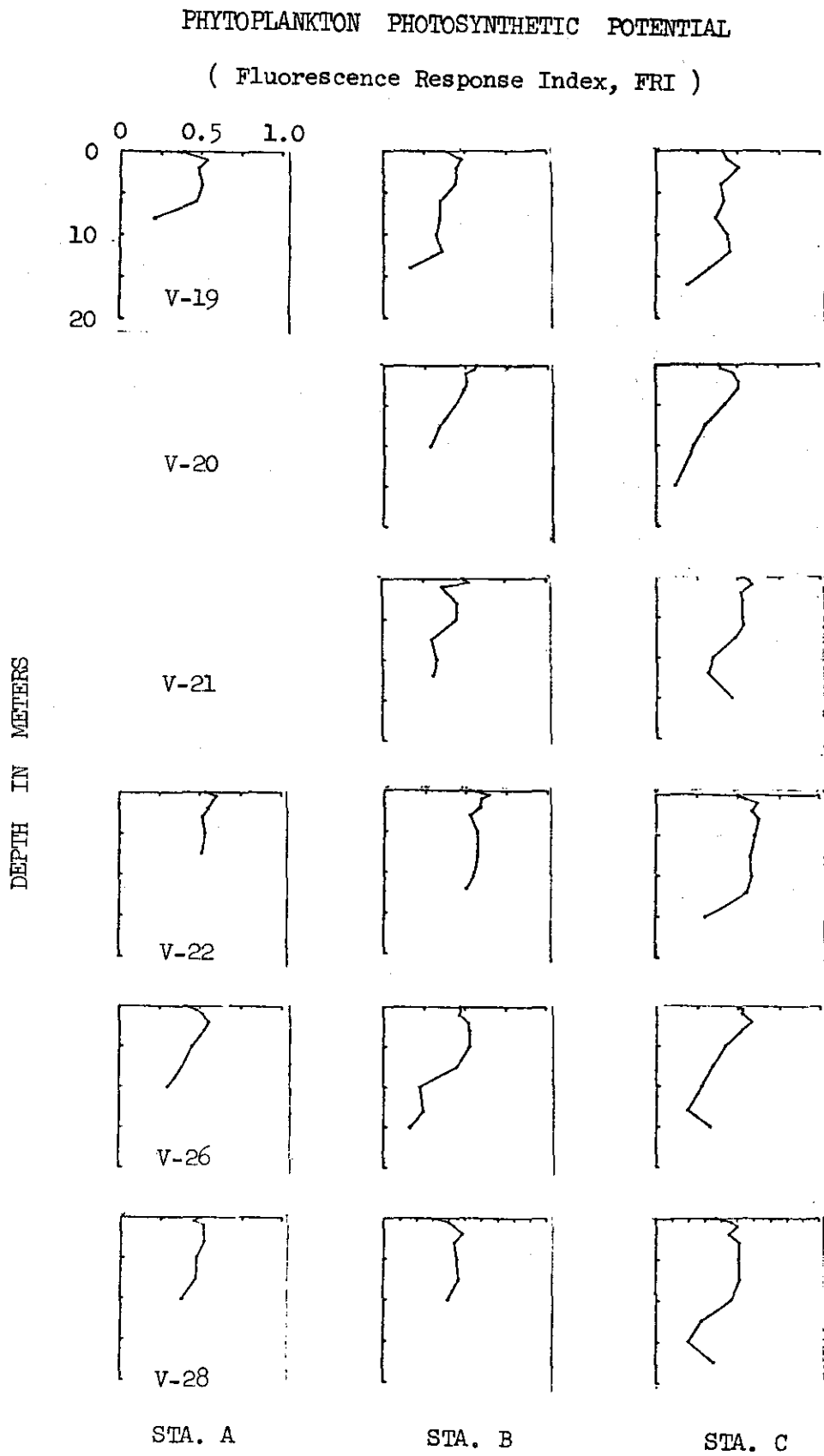
( Fluoresc. Units,  $F_i$  and  $F_d$  in cps )

Fig. 26 e.



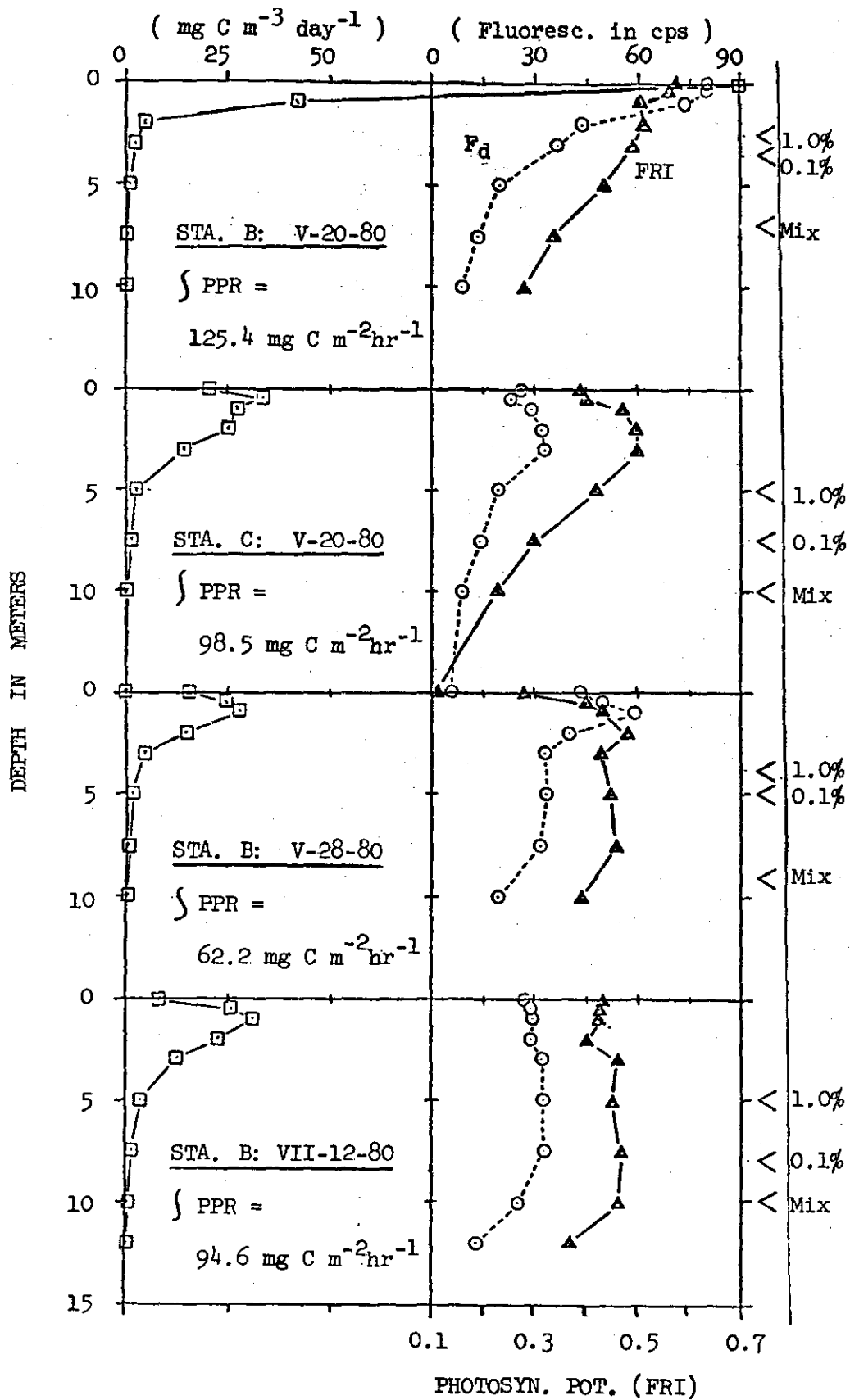


Figure 27. Phytoplankton productivity, photochemical capacity (FRI), and biomass ( $F_d$ ) within (sta. B) and outside (sta. C) a turbidity plume on V-20-80, following an inflow event (sta. B: V-28-80) and in mid-summer (sta. B: VII-12-80).

within (station B) and outside (station C) the turbidity plume produced by watershed inflow. The euphotic zone depth (i.e., depth of 1% surface light) at station B, which the turbidity plume had just reached on May 20, was 2.5 m, and was approximately 5 m at station C (Fig. 25). Vertical profiles show clearly that near-surface phytoplankton productivity at station B was enhanced by watershed inflow, presumably due to the combined effects of nutrient stimulation and reduced photoinhibition. Surface photosynthesis rates at stations B and C were 145 and 21 mg C m<sup>-3</sup> hr<sup>-1</sup>, respectively. Even though subsurface light availability was reduced at station B due to increased abiotic turbidity, integral water column phytoplankton productivity (i.e., in mg C m<sup>-2</sup> hr<sup>-1</sup>) exceeded that at the less turbid station C. Turbidity decreased and integral phytoplankton productivity declined at station B to about one-half its May 20 value by May 28, and the vertical distribution of photosynthesis had become characteristic of the profile retained throughout mid-summer (Fig. 27).

Tilzer et al. (1976) reported similar results from productivity measurements made within and outside a turbidity plume in Lake Tahoe. Surface and near-surface samples incubated in non-turbid water were more strongly photoinhibited than samples incubated within the turbid plume. However, within the plume, photosynthesis rates decreased more rapidly with depth due to increased light extinction. In contrast to our Lake Texoma comparisons, integral photosynthetic production in Lake Tahoe was suppressed within the sediment plume despite reduced light inhibition at the surface, because of light extinction and rapidly decreased photosynthesis rates with increased depth.

Dual-isotopic labelling of 2-m samples from stations B and C on May 20 was combined with size-fractionation filtration procedures to determine the effects of turbid watershed inflow on the in situ size distributions of autotrophy and microheterotrophy (see Section 3.4 for methods). A smaller fraction of the total autotrophic activity was associated with the 0.8-3.0  $\mu\text{m}$  size fraction at station B within the plume (Table 6), again indicating that river-transported suspended particulate matter, much of which is comprised of fine clay and silt particles in the 1-5  $\mu\text{m}$  size range, exerts a detrimental effect on small (ultraplankton-size,  $< 3 \mu\text{m}$ ) phytoplankton cells. Although vertical displacement of algal chlorophyll in the water column was not evident during the May 19-28 inflow period, as it had been in June 1979 (Fig. 23), these size fractionation results parallel those obtained during simulated watershed inflow experiments (see Section 4.2, Fig. 14). Microheterotrophy size distributions at stations B and C yielded similar implications (i.e., a shift toward larger size fractions in the presence of suspended particles; Table 6), and further support the hypothesis that ultra-phytoplankton and free-living bacteria (ca.  $< 3 \mu\text{m}$ ) are coflocculated by suspended silt and clay particles introduced with watershed runoff.

Microorganism-particle interactions are better known from investigations of soils than from aquatic systems. However, it is recognized that in the aqueous phase of soils or sediments, bacteria may be reversibly or irreversibly sorbed at solid surfaces, enveloped in colloidal material, and coflocculated with particulates of comparable size (Marshall 1980). In estuarine systems, both microorganisms and river-borne suspended particulates in freshwater inflows tend to flocculate and sediment as salinity increases (Marshall 1980). Although similar processes might be postulated for Lake

Table 6. Size distribution of planktonic autotrophic and microheterotrophic activities within a turbidity plume (station B) and outside the turbidity plume (station C) in Lake Texoma, 20 May 1980. Samples from 2-m depth, water temperature at both stations = 22°C. PPR = in situ phytoplankton productivity in  $\text{mg C m}^{-3} \text{ hr}^{-1}$ , RMA = relative microheterotrophic activity in  $\text{dpm} \times 10^3 \text{ subsample}^{-1}$ .

Station	Secchi Depth (m)	PPR	Percent of Total Activity Retained			
			0.2-0.8	0.8-3.0	3.0-8.0	8.0 $\mu\text{m}$
<u>AUTOTROPHIC ACTIVITY:</u>						
B (in plume)	0.5	25.0	0	5.4	62.7	31.9
C (not in plume)	1.2	4.0	0	31.1	46.5	22.4
<u>MICROHETEROTROPHIC ACTIVITY:</u>						
B (in plume)	0.5	280	52.7	42.9	3.6	0.8
C (not in plume)	1.2	226	84.3	13.3	2.4	0

Texoma, which is unusually saline for a freshwater system (conductance  $\approx 2000 \mu\text{mhos cm}^{-1}$ ), salinity-controlled processes cannot explain the vertical displacement of algal biomass observed in our watershed runoff experiments in 1979 (see Fig. 13), in which low-conductance well water was used. Clearly, additional experimentation will be required to identify the specific mechanisms underlying the interactions of river-transported particles and reservoir planktonic microorganisms, and to further examine the ecological implications of those interactions.

#### 4.4. General Discussion

The influence of riverine inflow on lacustrine systems has long been studied (e.g., see Hutchinson 1957, p. 295), especially in regard to the physical effects of density currents in lakes (Forel 1895, Numann 1938, Dussart 1948) and reservoirs (Weibe 1939a,b, 1940, 1941; Anderson and Pritchard 1951). Prior to the research reported here, few studies had directly addressed the interacting effects of river-transported nutrients and suspended particles on lacustrine phytoplankton and bacterioplankton activity (e.g., see Farnworth et al. 1979, who recently reviewed extant information on impacts of sediment and nutrients on biota in U.S. surface waters). Fortunately, joint studies conducted by the University of California (Davis) Tahoe Research Group and the NASA Ames Research Center on the influence of the Upper Truckee River sediment plume on eutrophication of Lake Tahoe provide some basis for comparison. Indeed, comparison of the Lake Tahoe and Lake Texoma results is of particular value for evaluating the relative impacts of watershed inflow and nutrient-particle loading events in oligotrophic and eutrophic systems.



Lake Tahoe is one of the most transparent (mid-lake Secchi depth = 20-40 m, 1% surface light = 80-90 m) and least productive lakes in the world. Lake Tahoe is ultraoligotrophic (i.e., extremely nutrient-poor), and phytoplankton production is limited by  $\text{NO}_3\text{-N}$ ,  $\text{PO}_4\text{-P}$  and Fe availability. Tilzer et al. (1976) reported that although inflowing nutrients and abiotic turbidity stimulated phytoplankton productivity and decreased photoinhibition in near-surface waters, respectively, watershed inflow resulted primarily in a major reduction of euphotic zone depth (e.g., from 80 m to 5 m). Eutrophic Lake Texoma remains relatively turbid (Secchi depth = 1-2 m, 1% surface light = 3-5 m; e.g., see Figs. 5,6,27) throughout the year due to high levels of biotically-produced particles (primarily, phytoplankton and phytoplankton-derived detritus). Turbid watershed inflow to Lake Texoma produces the same basic effects as in Lake Tahoe (i.e.; increased nutrient availability and decreased light availability, surface inhibition is reduced and light limitation in deeper strata becomes more severe); however, increased abiotic turbidity results in only a minor reduction in euphotic layer depth in productive water columns (e.g., in Lake Texoma) relative to transparent, unproductive water columns (e.g., in Lake Tahoe).

Turbid watershed inflow to Lake Tahoe resulted in the stimulation of both photosynthetic production and bacterial heterotrophy (Paerl and Goldman 1972 a,b, Paerl 1973, Goldman et al. 1974). Paerl and Goldman (1972 a,b) concluded that suspended silt particles in Lake Tahoe provided an excellent substrate for planktonic bacteria, and stimulated bacterial activity by increasing nutrient availability, concentrating dissolved organic materials by adsorption and providing attachment surfaces. Rela-

tive microheterotrophic activity was 25% greater in plume than in non-plume samples in Lake Texoma, thus indicating only a minor stimulation of microheterotrophy by watershed inflow as compared to the six-fold increase observed for autotrophy (Table 6). Although a slight tendency exists for increased bacterial attachment to larger particles in areas of higher suspended particle concentration, microheterotrophic activity in reservoir plankton communities appears to be rather consistently dominated by free-living rather than attached bacteria (Kimmel, in prep.). Since free-living bacteria are usually much less efficiently collected by zooplankton grazers than are small algal cells, this result has potentially important implications for the significance of dissolved allochthonous organic matter and bacterial contributions to the reservoir foodweb (Kimmel 1981).

## 5. PROJECT SUMMARY AND CONCLUSIONS

Land-water interactions are important determinants of water quality and trophic structure in reservoir ecosystems. An understanding of watershed-reservoir interactions is essential for predicting water quality and the ecological consequences of altering land-use patterns, agricultural practices, or the extent of urban and/or recreational development within reservoir watersheds. Improved knowledge of watershed runoff effects on reservoir productivity and water quality is particularly important for the U.S. Great Plains region where (1) man-made impoundments represent primary resources for surface water supply and water-based recreation, and (2) non-point source inputs via watershed runoff constitute the major contributions to reservoir nutrient loading. The primary goal of this research was to determine the effects of introduced nutrients and suspended particles on organic matter production in man-made impoundments. Specific research objectives were:

- (1) to experimentally evaluate the effects of suspended soil particles and nutrient-particle interactions on algal and bacterial activities and distribution, and
- (2) to examine in situ the effects of turbid watershed inflows on organic matter production by naturally occurring assemblages of reservoir phytoplankton and bacteria.

DCMU-enhanced in vivo chlorophyll fluorescence was evaluated, and then applied in experiments and field studies as an indicator of the photochemical capacity of reservoir phytoplankton. DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea) is a specific inhibitor of non-cyclic photosynthetic electron transport. Determination of in vivo chlorophyll

fluorescence before and after DCMU poisoning of a sample provides an indication of the photosynthetic electron transport activity. Our laboratory-field evaluation showed that measurement of the in vivo chlorophyll fluorescence response to DCMU provided valuable ecological information on phytoplankton physiological status in situ, and was applicable to field investigations of naturally-occurring phytoplankton assemblages. Parallel measurements of photosynthetically-active radiation, physical-chemical characteristics, photosynthetic carbon fixation, and DCMU-enhanced chlorophyll fluorescence response in several limnologically-dissimilar reservoirs permitted comparison of in situ effects of various light-nutrient-mixing regimes on phytoplankton productivity, physiological status and vertical distribution.

The fluorescence response technique, in combination with physical-chemical measurements and photosynthesis rate estimates, was applied to the examination of the effects of introduced nutrients and suspended particles accompanying watershed runoff on reservoir productivity. The investigation had two components: (1) enrichment experiments in which simulated watershed runoff was added to natural phytoplankton assemblages, and (2) field measurements during periods of watershed inflow to Lake Texoma.

Experiments were conducted at the USDA Southern Plains Watershed and Water Quality Laboratory (Durant, OK), and at the University of Oklahoma Biological Station (UOBS) on Lake Texoma. Light availability, phytoplankton photosynthesis, algal biomass and phytoplankton fluorescence response were monitored during experimental enrichments of ~~isolated~~ water columns (in model ponds at the USDA laboratory, and in Lake Texoma at the UOBS) with

simulated watershed runoff containing suspended particles of two different soils: San Saba clay and Bowie loam. Additionally, bioassay experiments were conducted with simulated runoff and filtered runoff (i.e., containing nutrients and organic compounds leached from the soils, but no soil particles). Experimental results are listed below:

- 1) Suspended particles introduced with watershed runoff reduced phytoplankton productivity and photochemical capacity by restricting light penetration into the water column. San Saba clay runoff caused higher light extinction and more persistent turbidity than did Bowie loam runoff.
- 2) Biologically-available nutrients associated with simulated watershed runoff (particularly with San Saba clay), stimulated phytoplankton productivity and enhanced algal photochemical capacity by increasing nutrient availability.
- 3) Introductions of high turbidity runoff to experimental water columns resulted in the vertical displacement of phytoplankton cells, apparently associated with clay particle flocculation and sedimentation. The addition of less turbid runoff did not remove algae from the water column.
- 4) In bioassay experiments, San Saba clay runoff additions resulted in higher algal photosynthesis rates and biomass increases than did Bowie loam runoff, presumably due to greater nutrient desorption from the San Saba clay. Algal production was higher in the presence of clay particles than in San Saba clay nutrient leachate, indicating continued nutrient exchange from the clay accompanying dissolved nutrient removal via algal and/or bacterial uptake.
- 5) Experimental runoff additions resulted in a shift in the size distribution of microheterotrophic activity from 0.4-0.8  $\mu\text{m}$  to 3.0-8.0  $\mu\text{m}$  particles,

indicating an association (probably due to cocollocculation) of formerly free-living bacteria with clay particles. Very little microheterotrophic activity was associated with particles  $> 8 \mu\text{m}$ .

Field measurements conducted during periods of watershed runoff and inflow to Lake Texoma in 1979 and 1980 revealed patterns similar to those observed in experiments. Turbid watershed runoff produced an initial reduction in phytoplankton productivity within the water column attributable to decreased light penetration. Vertical profiles of in situ phytoplankton productivity within and outside of a turbidity plume in Lake Texoma showed that decreased photosynthetic activity was due primarily to the reduced thickness of the euphotic layer, as carbon fixation at  $> 1\%$  surface light levels within the plume was stimulated by the increased nutrient availability accompanying the inflow. Very turbid inflow in 1979 resulted in the vertical displacement of phytoplankton from the water column similar to that observed experimentally. Less turbid inflow did not produce as marked an effect either in experiments or in Lake Texoma in 1980, suggesting that particle concentration thresholds probably exist for phytoplankton-bacterial flocculation by clay particles.

The ecological effects of watershed runoff events are certain to be extremely variable in nature because: (1) different soils possess differing mechanical, compositional and sorption characteristics, (2) runoff from different watersheds is composed of varying combinations of soils and soil types, (3) chemical and biological characteristics of the receiving water bodies differ tremendously, and (4) biological responses appear to vary with soil type and the particle concentration of the runoff. However, in isolated water column experiments and in Lake Texoma, the phytoplankton-bacterial response to turbid watershed inflow occurred in three distinct phases:

- (1) light limitation of photosynthetic activity,
- (2) removal of phytoplankton and bacterial cells from the water column, presumably by flocculation and sedimentation with silt and clay particles (such removal was detected only in association with high suspended soil particle concentrations), and
- (3) nutrient stimulation of photosynthetic activity of phytoplankton remaining in the water column (nutrient stimulation did not occur until until particle sedimentation reduced turbidity to the extent that light availability was no longer the most limiting factor for algal photosynthesis).

This basic sequence occurs temporally at a given location and depth, vertically within the water column at a given location, and longitudinally within water bodies having some degree of directional flow (e.g., reservoirs). Indeed, analogous effects on the vertical distribution of phytoplankton photosynthesis and integral production rates should be expected to occur in different portions of lakes, reservoirs and estuaries possessing marked longitudinal gradients in turbidity, nutrient availability and productivity.

As stated in the introduction (Section 1), this investigation was designed to answer the following questions:

- (1) Does the introduction of silt and clay particles to the reservoir water column reduce water transparency to such a degree that phytoplankton photosynthesis becomes limited by light availability?
- (2) Does the introduction of dissolved nutrients in runoff water and desorption of nutrients from suspended silts and clays increase nutrient availability, and thereby stimulate organic matter production by phytoplankton and bacteria?

(3) Does the presence of suspended silts and clays stimulate microbial activity by concentrating dissolved organic compounds via adsorption and then functioning as both surface and substrate for the growth of attached microorganisms?

(4) Does turbid watershed inflow modify the availability of microheterotrophic production to grazers via bacterial attachment to or aggregation with silt and clay particles in the water column?

Question 1: Watershed runoff experiments and in situ monitoring of watershed runoff events in Lake Texoma showed that turbidity produced by river-borne suspended particles reduces the thickness of the euphotic layer, and thereby results in light limitation of phytoplankton photosynthesis within a larger portion of the water column (Table 4, Figs. 22, 26, 27).

Question 2: Nutrient desorption from suspended silt and clay particles can greatly enhance nutrient availability for phytoplankton and bacterial production, but varies with soil type (Figs. 17 and 18). Increased nutrient availability associated with watershed inflow stimulates phytoplankton production within the euphotic portion of the water column and, in combination reduced algal photoinhibition in near-surface layers, may result in enhanced integral production (Fig. 27).

Questions 3 and 4: The presence of suspended particles did not appear to have a major stimulatory effect on microheterotrophic activity, but did result in a shift toward larger particle sizes in both autotrophic and microheterotrophic activities (Figs. 14, 19, Table 6). Although such a shift in size distributions would tend to make ultraphytoplankton and free-living bacteria temporarily more available to planktonic grazers by increasing the effective particle sizes, concurrent increases in settling



rates and the dilution of suspended organic particulates by high concentrations of silt and clay particles likely results in (i) a net reduction of available trophic resources within the water column, and (ii) a net displacement of both allochthonous and autochthonous organic particles from the water column to the bottom sediments.

In Great Plains reservoirs, many of which receive drainage from large, erodable watersheds dominated by clay soils, seasonal watershed inflow events are of major ecological significance by virtue of (i) large nutrient inputs to the lacustrine system, (ii) rapid vertical displacement of organic materials (healthy algal and bacterial cells, in addition to allochthonous organic particles) from the water column to benthic regions, and (iii) the "resetting" of physical-chemical conditions and planktonic community structure. The latter aspect may be particularly significant in altering patterns of phytoplankton community succession if the removal of algal cells from the water column by algal-clay coflocculation and sedimentation proves to be a selective process.

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