ALGAL RESPONSE TO NUTRIENTS IN A TURBID STREAM MESOCOSM

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PREFACE

The two most prevalent forms of surface water non-point source pollution in North America are nutrients and sediment. This study was conducted to explore how light attenuation caused by suspended sediments affects a biomonitoring system of nutrient-diffusing periphytometers. Algal response to nutrients was measured as biomass (chlorophyll *a*) and as chlorophyll *c*:*a* ratio. Various conditions were employed to explore the possible use of these measurements to evaluate water quality in terms of nutrient and sediment loading.

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CHAPTER I

INTRODUCTION

Aquatic Plants

Aquatic plants are a diverse group including macrophytes, which are large enough to see without magnification, and microscopic plants (algae). Algae can be generally divided into plankton, which float in the water column, and periphyton, which are attached to some substrate - sediment, rocks, other plants, even to animals.

A host of complex interactive factors affect aquatic plants. In the language of the Clean Water Act (WEF, 1987), they include chemical, physical, and biological factors. Chemical factors include pH, nutrients, pesticides, metals, and organic matter. When erosion occurs, chemical pollutants in the soil potentially end up in the water. Physical factors include suspended sediment, basin morphometry, flow rate of streams, residence time of lakes, temperature, solar radiation and other climatic factors. Biological factors include competing plants and herbivores. Sediments play a role in most of these factors which impact macrophytes and algae. Of particular concern for this study is the role of suspended sediments in eutrophication assessment.

Justification

In the United States, the quality of surface water does not always fully support its designated use. Sediment and nutrients are the main culprits, followed by metals, pesticides, priority chemicals, organic enrichment, and pathogens. Good water quality assessment is the essential first step in managing pollutants.

Biological *in situ* water quality indicators are preferable to *in vitro* assays or chemical analyses because they entail fewer constraints based on limited species or a single grab sample. One *in situ* method is use of periphytometers. A periphytometer is an artificial algal colonizing surface which is placed in a stream for a time. The accumulated algae are then removed and biomass quantified. This study examined the possible biomonitoring use of a new type of periphytometer with respect to sediments and nutrients. This thesis focuses on the effect of light reduction due to suspended sediments, primarily montmorillonite clay, on algal response to nutrients.

Hypotheses

The question of interest to biomonitoring activities is whether light attenuation caused by suspended sediment changes algal response to nutrients.

I expect more biomass on periphytometers that provide nutrients that are otherwise limiting in ambient water. I expect different chlorophyll ratios in response to different nutrient solutions because of nutrient requirements of algal taxonomic groups. I expect less biomass on the periphytometers with the most light attenuation. The chlorophyll ratios should be different under different light

treatments because of different light requirements of taxonomic groups and possible acclimation. The null hypotheses are:

1) Algal biomass responses to different nutrient treatments are equal.

2) Algal chlorophyll *c*:*a* ratio responses to different nutrient treatments are equal.

3) Algal biomass responses to different light treatments are equal.

4) Algal chlorophyll *c*:*a* ratio responses to different light treatments are equal.

5) Algal biomass responses to combinations of nutrient and light treatments are equal.

6) Algal chlorophyll *c*:*a* ratio responses to combinations of nutrient and light treatments are equal.

CHAPTER II

LITERATURE REVIEW

Factors Affecting Aquatic Plants

The aquatic environment requires specific adaptations. Nutrients are in low concentration compared to the soil environment. Availability of O_2 for respiration and CO_2 for photosynthesis is limited in water. Light is attenuated by canopy, the water itself, and by substances in it. Suspended sediments impact nutrient and light availability by chemical, physical, and biological factors.

Chemical - Chemical factors include pH, nutrients, pesticides, metals, and organic matter.

Soil pH affects nutrient availability (Foth, 1984) and metal toxicity through complexation reactions and solubility of nutrients, metals, and organic compounds (Bohn et al., 1985) and controls biological/redox transformations of combined N, P, and organic compounds (Wetzel, 1983). There is some question, though, if small differences in pH affect nutrient uptake (Toetz, 1981). Metals associated with sediments can accumulate in macrophytes or change algal characteristics (Munawar et al., 1983; Whitton et. al., 1989). Lower pH causes

metals to be more bioavailable (Bohn et al., 1985). Clays can be a source of acidity (Foth, 1984).

Nutrient concentration has well-known connections to trophic status, taxonomic distribution and biomass. Phosphorus is associated with sediment in the process known as phosphorus enrichment. As larger soil particles settle to the bottom, phosphorus bound to clay particles in the water column potentially become bioavailable (Sharpley, 1980). Silicon is a nutritional requirement for diatoms, a large class of algae (Bacillariophyceae) which grow a silicious frustule. There has been shown a direct relationship between the availability of silicon and abundance of diatoms (Wetzel, 1983). Silicon comes from aging of alumino-silicate clays (Bohn et al., 1985). Montmorillonite is one such clay and is the main type found in Lake Carl Blackwell's drainage (USDA-SCS, 1987). Dinoflagellate algae (Pyrrhophyta) are armored with cellulose plates (Bold and Wynne, 1978) and so presumably have a high requirement for carbon, which may have an organic or inorganic source. Low nitrogen to phosphorus ratios in the water column favor N_2-fixing cyanobacteria algae over other phytoplankton (Wetzel, 1983), especially in low light conditions (Smith, 1986). Marks and Lowe (1993) found species dominance changes among diatoms in relation to light and nutrient interactions. Oxygen levels, whether biogenic or a result of turbulence, affect form and location of P, Fe, Mn, Ca, C, and more, in the water body (Bates and Neafus, 1978; Wetzel, 1983; Bohn et al., 1985). In general, as nutrient levels and ratios change, species composition changes (Shubert, 1984).

The chemistry of pesticides is reflected in quantity, form (breakdown product), and timelength they are in the water (Biehl and Buck, 1987). Insecticides can alter aquatic invertebrate grazing activity, which can have a top-down impact on plants, and herbicides can directly alter genetic diversity or gene pool

composition (Hobin, unpublished). Clays suspended in the water adsorb some pesticides via ion exchange (Miltner et al., 1987). Plant responses vary widely with taxa, and so chemical factors like these and others can determine distribution of taxa and the productivity of those present (Haslam, 1987).

Physical - Physical factors include sediment, basin morphometry, flow rate of streams, temperature, solar radiation and other climatic factors such as wind and rainfall patterns.

Sediment can be viewed in two ways - as a substrate for rooted plants and benthic periphyton, and as suspended solids. Particle size can influence stability of the substrate and its rooted occupants. Smaller particle size can increase phosphorous bioavailability (Sharpley, 1980; Dorich et al., 1984). Particle size is a factor in settling time and therefore in turbidity (Nolen et al., 1985). Smaller particles stay suspended longer. Particle size may influence productivity in relation to light availability as shown by DeNicola and Hoagland (1992), who reported higher productivity on sand compared to gravel under low light and the reverse in higher light.

Light also affects nutrient uptake (Varga et al., undated). Submerged macrophytes are most affected by turbidity (Haslam, 1987). Increases in turbidity select against submerged plants (Tanner et al., 1993), while emergent macrophytes such as pondweed (*Potamogeton*) may be able to compensate for a reduced euphotic (optimally photosynthetic) zone with floating leaves. In western European rivers, unspecified toxic pollution is often associated with turbidity (Haslam, 1987). One might conclude that submerged species may be at risk from those toxins in addition to light reduction.

Shallow lakes have larger littoral areas containing more rooted macrophytes than deeper, steeper-sided lakes (Wetzel, 1983). Lakes, or streams with pools may contain phytoplankton not found in flowing water (Hynes, 1970; Vannote et. al., 1980; Haraughty, 1995). Periphyton are the primary algae found in streams, especially of lower order (Allan, 1994). In general, the higher the flow rate, the less biomass. Some species have optimum flow rates which help determine species dominance of a particular niche (Patrick, 1948; Haslam, 1987; Ghosh and Gaur, 1990). Biggs and Hickey (1994) found decreasing biomass as flow rates increased from 0.14 to 0.38 m s^{-1}. Ghosh and Gaur (1990) did not address combined factors of flow rate and turbidity, which are often related (Thornton et al., 1990). There can also be longitudinal patterns in stream biomass; as contributing watershed area increases, turbidity may increase and stream productivity decrease (Munn et al., 1989).

Wind, combined with lake fetch and shallow depth, can produce uniformly turbid, oxygenated water, as is common in Oklahoma (Rodney and Stefan, 1984; Howick and Wilhm, 1985). Turbulence, caused by wind or flow, may resuspend deposited sediments, reducing light and possibly increasing nutrients, particularly phosphorus. Fluctuating water levels, such as occurs in alternating wet and dry seasons or below hydroelectric structures, select against some plants. High intensity rainfall events increase sediment loading in runoff.

Cooler temperatures are generally favorable to diatoms, while warmer temperatures increase many plants' photosynthetic capabilities. This can be seen in the seasonality of taxonomic dominance (Wetzel, 1983). Suspended sediment may act in opposing directions as it absorbs radiant energy, which warms the water, and reduces light available to plants. Change in albedo (reflectivity) of the water, if any, would be due to the nature of the clay particles,

which scatter light uniformly rather than reflect it back out of the water. Increased temperature correlates positively with growth and grazing pressure (Shubert, 1984).

Biological - Biological factors include competing plants and grazers, such as zooplankton, invertebrates, and fish.

Carp and drum (two herbivorous fish species) were implicated in one study as reducing macrophyte biomass, under conditions of fluctuating water levels, turbidity, and eutrophication (Kahl, 1993). The author suggested that the fish provided a nutrient level sufficient to allow a dense population of phytoplankton which subsequently shaded the macrophytes.

While there is a top-down effect, aquatic plants certainly have a bottom-up effect, as well. Turbidity and lack of macrophyte habitat (which may itself result from turbidity) was implicated in low populations of a parasitic trematode in snails and fish (Spall, 1968). Because of turbidity or some other factor, low productivity in aquatic plants results in inadequate forage for fish (Muoneke et al., 1992). Algae and macrophytes produce oxygen, biomass, and often organic compounds, which are used by bacteria, other plants, and grazers. Macrophytes and algae may shade themselves or other species out, depending on other environmental factors (Agusti, 1991). The canopy of forested streams influences the quality and quantity of light reaching the water (DeNicola and Hoagland, 1992). A complex interaction occurs between the size, physiological strategies, and habitat of plants and that of consumers that depend on them (Wetzel, 1983).

Pollution Status and Assessment

According to the EPA (1992), only 56% of assessed river miles and 43% of assessed lake acres fully support their designated use.

Sediment

Nationally, sediment is a pollutant in 45% of impaired rivers, and in 22% of impaired lakes (EPA, 1992). Sediments reduce water clarity, impact municipal drinking water treatment systems, and affect biota directly and by habitat alteration.

Nutrients

Nutrient pollution impacts 37% of assessed river miles and 40% of assessed lake acres (EPA, 1992). Excess nutrients, particularly phosphorus, can cause algal blooms. The subsequent decay and microbial respiration deplete oxygen, causing fish kills. Certain algae, particularly cyanobacteria but several other classes as well, contribute to objectionable odor and/or taste in drinking water (Terrell and Perfetti, 1988). While masses of algae may annoy anglers or swimmers or simply be aesthetically displeasing, they benefit the ecosystem by encouraging invertebrate biomass and species diversity and by providing habitat for fish.

Aquatic plants as biomonitors

The goal of section 101 of PL 92-500, known as the Clean Water Act Amendments of 1972, is to restore and maintain the chemical, physical, and biological integrity of the nation's waters (WEF, 1987).

Several biological *in situ* water quality assessment methods have been developed. Fish and invertebrate species statistics have been used to assess stream quality (Beck, 1954; Karr, 1981). The bioaccumulating qualities of fish and algae have been used to estimate heavy metals such as mercury and lead in waters (Whitton et al., 1989; Pigg, 1995). Algal communities have been associated with different levels of eutrophication or pollution status of water (Patrick, 1948; Terrell and Perfetti, 1988). The taxonomic expertise required to identify algae to species is not common.

Another *in situ* method is use of periphytometers. The algae which colonize the periphytometers can be identified or biomass can be quantified as dry weight or as chlorophyll. Many kinds of periphytometers have been used, including natural rocks or sand. Naturally-occuring macrophytes or macroalgae can host epiphytic algae. Artificial periphytometers include styrofoam, glass slides, clay tiles, and nutrient-diffusing substrates, each of which has its limitations (Aloi, 1990). Whitton and Kelly (1995) doubt the usefulness of periphyton biomass measurement in community-based river monitoring.

Natural materials have variable surface texture or geometry, creating statistical and logistical sampling problems. Recovery by brushing or scraping can result in sample loss. Loosely attached epiphytic algae can be lost during sampling, and tightly-attached algae may be difficult to dislodge for analysis. Microscopic examination is possible only with low densities.

Artificial substrates have the advantage of a homogeneous surface. However, algae colonizing them may, but usually do not, represent the natural community. Rough surfaces are colonized more readily than smooth glass. Among nutrient-diffusing periphytometers are clay flowerpots or sand, augmented with a solidified nutrient-agar. Algae penetrate the clay substrate so that complete recovery is not possible. Algae penetrate glass fiber filters, but sample recovery is complete when the chlorophyll is extracted. Minimal handling, as in Matlock Periphytometers (Matlock, 1996), promises recovery that is independent of investigator variability.

Field experiments are typically at the mercy of weather and vandalism (Matlock, 1996). Stream morphology imposes limitations on experimental design. Mesocosm experiments attempt to imitate the natural environment and at the same time eliminate or isolate as many variables as possible.

Taxonomic distribution may be estimated in part by relative amounts of pigments. Although all algae contain chlorophyll *a*, Chrysophytes, including diatoms (Bacillariophyceae) and dinoflagellates (Dinophyta) have chlorophyll *c* but not *b*. Bluegreens (Cyanobacteria) have neither *b* nor *c*. Green algae (Chlorophyta) is the only taxon containing chlorophyll *b* (Bold and Wynne, 1978).

Algal taxa are characterized by different light and nutrient requirements. Theoretically, responses to different nutrient treatments contain information about sediment and nutrient loading through biomass and through taxonomic distribution as pigment ratios. Falkowski and Owens (1980) demonstrated light levels to impact chlorophyll ratios in diatoms and green algae. Chlorophyll *b:a* ratios ranged from 0.50 to 0.18 for greens, and *c:a* ratios ranged from 0.53 to 0.17 for diatoms (Falkowski and Owens, 1980). In both cases, the amount of

accessory pigment (chlorophyll *b* or *c*) increased relative to chlorophyll *a* as light decreased.

Reduced light levels may be caused by suspended solids or dissolved substances, but within the limits of the present study, reduced light is assumed to be caused by suspended sediment and might be qualitatively analyzed using taxonomic distribution. In the case of fluctuating turbidity, chlorophyll ratio might be used to evaluate typical conditions. For example, green algae and some cyanobacteria have a high light requirement and diatoms a low requirement for, even intolerance of, intense light. Dominance by diatoms, then, could indicate a turbid waterbody. In the event a stream with uneven canopy were being evaluated with this method, block replicates would be placed in representative areas of the stream. Understanding sediment effects on plants or on a method might help provide a means to assess water quality.

Taxonomic distribution may also be estimated by responses to nutrients, rather than the traditional method of identifying species of varying pollution-tolerance levels (Palmer, 1969). Cyanobacteria have a low nitrogen requirement because of an ability to fix atmospheric N_2. A response to phosphorus but not to nitrogen, coupled with a low chlorophyll *x:a* ratio would be two clues to dominance by Cyanobacteria. Diatoms generally have a low phosphorus requirement so they would not respond greatly to added phosphorus. Green algae are often associated with eutrophic conditions (Wetzel, 1983) so would respond to added nitrogen and phosphorus. Niederhauser and Schanz (1993), through chlorophyll *b:c* ratios which were supported by microscopic examination, found that green algae responded to nitrogen, phosphorus, and carbon enrichments in a diatom-dominated oligotrophic lake. They also found diatom species shifts with carbon treatments.

Any single nutrient does not promote algal growth; plants, including algae, need complete available nutrients. Limiting nutrients are those which are present in too low of a concentration to support maximum growth. Addition of the limiting nutrient to the ecosystem will cause an increase in algal biomass in the absence of counteracting grazing. Nutrient-diffusing periphytometers incorporate different nutrients and permit identification of the limiting nutrient based on differential biomass accumulation. A nutrient-diffusing periphytometer enables identification of limiting nutrients, thereby allowing use of algae as a nutrient pollution biomonitor.

Nutrient and Sediment Pollution Prevention

Agriculture impacts 72% of assessed river miles and 56% of assessed lake acres (EPA, 1992). This is noteworthy for two reasons: it indicates the loss of valuable soil from production, and the erosion into waterbodies of pollutants associated with agricultural soils (nutrients and pesticides). Sediment pollution also has important sources in hydrologic or habitat modification, resource extraction, and construction (Brabander et. al., 1985; EPA, 1992; Brown et. al., 1993; Christensen et. al., 1993). Nutrients also come from horticultural or silvicultural enterprises, municipal point sources and urban runoff (EPA, 1992).

As the primary source of non-point source (NPS) pollution, agriculture bears scrutiny for pollution prevention methods. Sediment from eroded agricultural land is itself sometimes a source of nutrient pollution, as in the case of phosphorus enrichment, or nutrients can be dissolved in runoff (Smith et. al., 1983). The usual term for practices that prevent this type of pollution is 'best management practices' or BMP's. The former USDA Soil Conservation Service (SCS), now

named Natural Resource Conservation Service (NRCS), acknowledges the need for an integrated ecosystem-based approach (Shaw, 1994) to protect water quality as well as conserve farmers' resources.

Several things can be done to control erosion and reduce sediment loss. Special planning must be undertaken for use of steep or highly erodible lands. Controlled grazing may be preferable to cropping, for instance, to maintain permanent cover. Conservation tillage practices reduce soil exposure to eroding elements. Even slight slopes have the potential for soil loss. Terraces and contour ridges can be built to slow flow from peak to vally. Grassed waterways trap soil lost from cropped land. Riparian buffer zones - wooded streamsides - trap sediment, prevent scouring from flood events, and act as nutrient sinks. Preserving the riparian buffer by limiting grazing animal access to surface water can reduce both sediment and nutrient loading, but upstream influences can overshadow local efforts (Platts and Nelson, 1985). Removal of cattle from rangeland during winter when vegetation is not growing (Van Keuren et. al., 1979; Owens et. al., 1983;), or grazing sheep instead of cattle (Lambert et. al., 1985; Lusby, 1989), has been shown to reduce sediment and nutrient inputs to surface water.

Nutrient pollution sources include municipal and animal wastes and fertilizers (EPA, 1992). Nutrient pollution is primarily a problem of phosphorus and nitrogen, which behave very differently in the environment. Phosphorus, in its various organic and inorganic forms, binds with soil particles, especially clay, so erosion is often phosphorus's main route into a waterbody as it leaves the crop to which it has been applied as fertilizer. It may then convert to bioavailable orthophosphate (Bohn et. al., 1985). It is mostly associated with eutrophication of non-flowing waters, partly because benthic sediments create a source-sink

situation and partly because of a lake's relatively long residence time, although it can also be a problem in lotic systems (Daniel et. al., 1994). Excess phosphorus is associated with nuisance bluegreen algae (Cyanobacteria) blooms because of some species' ability to fix atmospheric nitrogen. Control of erosion is one way to limit phosphorus loading of surface waters.

Nitrogen is much more mobile in the soil than phosphorus, and can enter waters through runoff, erosion, or percolation into the water table. Excess nitrogen is often associated with green algae blooms. However, both nitrogen and phosphorus are required for optimum growth.

Watershed and site computer simulation models help to predict erosion, sediment and nutrient loading. These NPS management tools include AGNPS (Agricultural Non-Point Source Pollution Model) (Young et. al., 1987) and USLE (Universal Soil Loss Equation) (Wischmeier and Smith, 1978) and its later versions as RUSLE (Revised USLE) and MUSLE (Modified USLE). The SIMPLE (Spatially Integrated Model for Phosphorus Loading and Erosion) model focuses on the major eutrophication element discussed above. As with any model, empirical measurements are made to validate, or affirm, the model's usefulness (Matlock et. al., 1994).

CHAPTER III

MATERIALS AND METHODS

Site

The study site is located at the USDA hydrology lab at Lake Carl Blackwell west of Stillwater, Oklahoma, a shallow, turbid, nutrient-poor flood-control reservoir of 1300 ha on the Stillwater Creek, built in 1937. Mean depth is 4.9 m and maximum depth is 14.5 m. Water level fluctuates considerably due to climate and low watershed:lake surface ratio (Howick and Wilhm, 1985). Watershed land use is mixed rural: range, cropland, recreation, and residences.

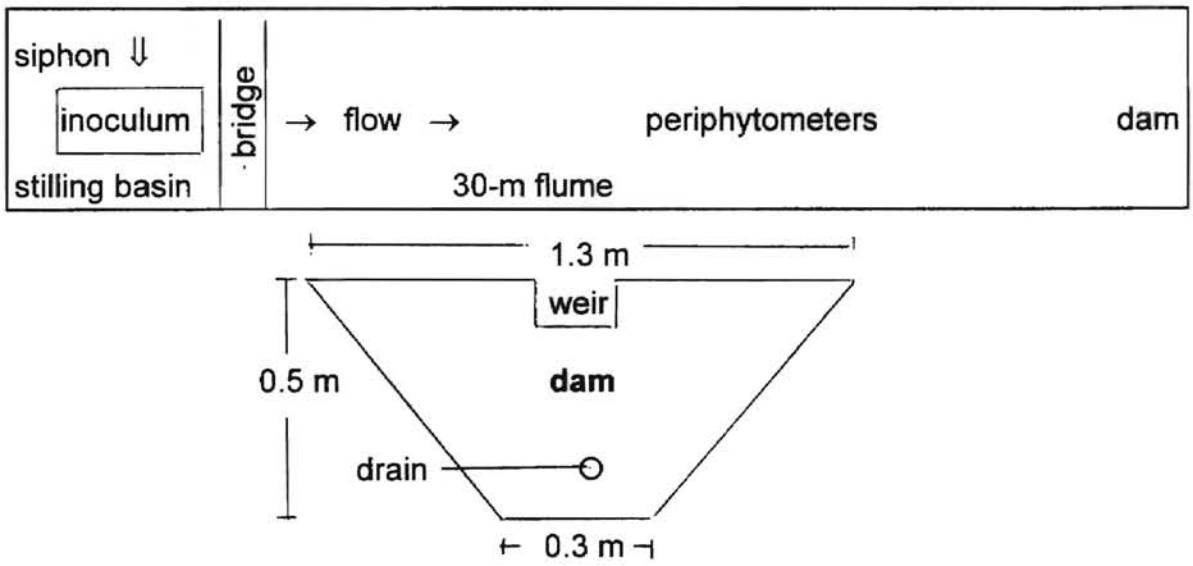

Figure 1. Concrete flume stream mesocosm, aerial and end views (not to scale).

A 30-m section of concrete flume simulated a stream run (Fig. 1) while excluding much of the naturally occurring variability. Siphons which fed the flume drew water through the dam at approximately 6 m depth. The flume water drawn through the siphon was low in biota, with pH of 7.5 - 8.5 and turbidity of 15 - 38 NTU throughout the experiments.

Some *Chara, Cladophora,* and pennate diatoms were found near the dam. The narrow (due to suspended sediment) euphotic zone rises and falls with fluctuating water levels.

A concrete block platform supporting algae-colonized rocks and providing aeration was used after nanoplankton samples in the first experiment study consistently revealed less than 50 algal organisms/ml and no zooplankton. Initially, lower dissolved oxygen (DO) measurements at the inlet compared to the outlet indicated oxygen entered the flume through atmospheric equilibration. DO was not measured later due to problems with the meter. Rocks colonized with diverse algal populations including diatoms, cyanobacteria, and green algae (especially *Cladophora*) were brought from the lake shore and from streams in the Illinois River drainage and spread on concrete blocks in a stilling basin under the siphon outlet (a 5 cm diameter faucet) to aerate the flume water and provide periphyton propagules.

Apparatus

A nutrient-diffusing periphytometer under development was used in these experiments (Matlock, 1996). The periphytometers, which were secured in aluminum racks on the bottom of the flume, consisted of 1-liter reservoirs (Cubitainer®) sealed with cellulose dialysis membrane (Spectra/Por®2, 12-14

kilodalton cutoff) and covered with a glass fiber filter (Whatman® 934-AH, nominal pore size 1.5 μm) (Fig. 2). The nutrient solutions diffused from the reservoir through the membrane. Algae colonized the filter surface. While Aloi's (1990) review of periphyton field methods does not include glass fiber filters as colonization surfaces, the standard method for determining chlorophyll in plankton uses them as collection material (APHA, 1989).

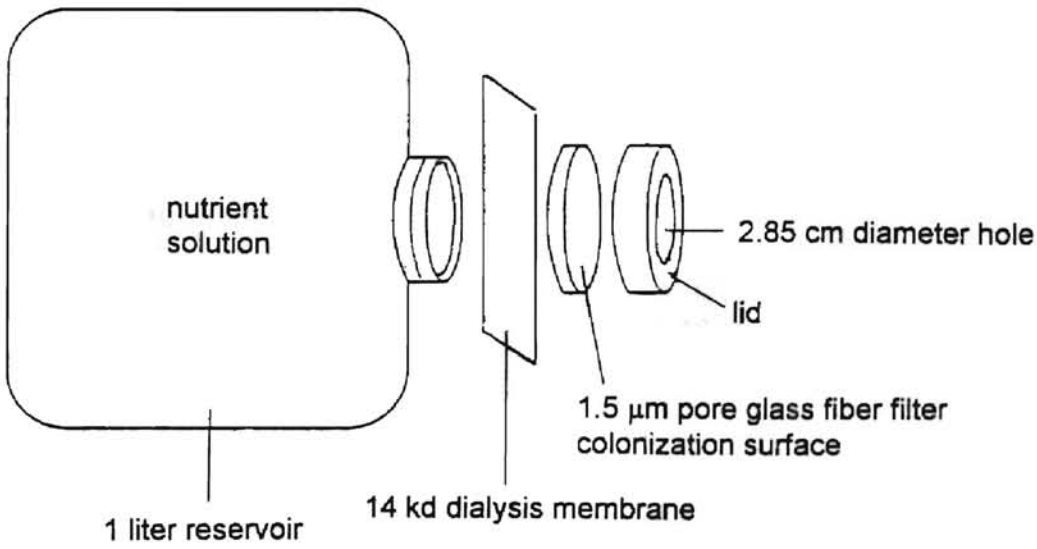

Figure 2. Nutrient-diffusing Matlock periphytometer. After Matlock (1996).

The six nutrient solutions were nitrogen (N), phosphorus (P), nitrogen and phosphorus (N+P), micronutrients (Micro), total nutrients (Total), and reverse osmosis water (Control). Where nitrogen and phosphorus are combined in a nutrient treatment (N+P and Total), the concentration of each is half that when alone. Table I lists the nutrient solutions and their concentrations. We assumed that carbon was not limiting. Montmorillonite is a source of silicon (Bohn et al.,

1985). Therefore no bicarbonate or silicon were included in the nutrient recipes. Except for the pilot and periphytometer periphyton identification, each solution included 15,000 units penicillin (AgriLabs® Twin-Pen™) per liter to prevent microbial digestion of the dialysis membrane.

Table I. Nutrient solutions contained in diffusing periphytometers.

solution name	chemical	conc. (mg l^{-1})
N (nitrogen)	$NaNO_3$	$3.00x10^2$
P (phosphorus)	K_2HPO_4	$5.00x10^2$
N+P	$NaNO_3$	$1.50x10^2$
	K_2HPO_4	$2.50x10^2$
Micro (micronutrients)	$MgCl_2 \cdot 6H_2O$	$2.44x10^3$
	$CaCl_2 \cdot 2H_2O$	$8.82x10^2$
	$MgSO_4$	$1.44x10^3$
	H_3BO_3	$3.70x10^1$
	$MnCl_2 \cdot 4H_2O$	$8.32x10^1$
	$ZnSO_4 \cdot 7H_2O$	$1.38x10^0$
	$CoCl_2 \cdot 6H_2O$	$2.86x10^{-1}$
	$CuCl_2 \cdot 2H_2O$	$2.40x10^{-3}$
	$MoO_3 \cdot H_2O$	$9.72x10^{-1}$
	$FeCl_3 \cdot 6H_2O$	$3.20x10^1$
	$Na_2EDTA \cdot 2H_2O$	$6.00x10^1$
Total	1/2 N + 1/2 P + 1/2 Micro	
Control	reverse osmosis H_2O	

Analyses

Chemical

Ambient concentrations of major nutrients were measured in the flume at the beginning and end of each experiment. Nitrate were measured by UV spectroscopy (Crumpton et al., 1992). Orthophosphate was measured following

APHA (1989) ascorbic acid method 424 F. No pH or conductivity was obtained, due to a meter malfunction.

Physical

Flow was measured using a 7.6 x 15.2 cm weir notch in the dam. Other physical measurements were made at the beginning and end of each experiment. Temperature was measured midday at the periphytometer colonization surface depth with a mercury thermometer. Sediment in the water column was measured as mg l^{-1} retained on Whatman GF/F glass fiber filters, nominal pore size 0.7 μm (APHA, 1989). Nephelometric turbidity was measured on a Hach 2100A Turbidimeter. Relative light levels were measured at midday using a LI-COR LI-1000 datalogger and radiation sensors LI-193SA at the periphytometer level and LI-192SA at the water surface.

Biological

Phytoplankton and periphyton were identified typically to genus using Prescott (1978), Bold and Wynne (1978), and Lee (1989). From July to October 1994, plankton were sampled from the lake, from the siphon, and from the flume. Subsurface samples were poured through a 10-μm mesh plankton net. They were counted following APHA (1989) procedures.

Periphyton were first sampled 15 September 1994 from inoculum materials and the flume walls. On 17 May 1995, periphyton were scraped from inoculum materials, from the flume walls just below and 30 cm below the surface. On 23 May a single rack of the 6 nutrient treatments was set in the flume for 12 days to

accumulate periphyton for identification. After removal from the reservoirs, the filters were wrapped in foil and placed on ice for transport to the lab. They were stored at 4 to 5 °C until identification the next day. Each filter was separated into halves and placed on a microscope slide as a wet mount for viewing at 200X. On 3 July, algae were sampled from the flume wall and masses floating midstream.

Trials suggested a 7- to 14-day incubation period for optimum biomass accumulation on the periphytometers (Matlock, 1996). After 7 to 9 days in the stream, the filters were placed in 4 ml of 90% alkylized acetone extraction solvent, and transported in a dark box to the laboratory for standard trichromatic spectrophotometric determination of chlorophylls *a, b*, and *c* (APHA, 1989). Method 10200H.2c was followed except that prior to the overnight cold dark extraction period, the collected filters were shaken vigorously 100 times in the capped centrifuge tubes because there was not time to grind the samples as recommended. In the pilot and Experiment #1 filters were placed in 5 ml solvent. A Shimadzu UV160U scanning spectrophotometer (bandwidth 2 nm) was used.

Although all three chlorophylls were measured, virtually no chlorophyll *b* was detected in the pilot or any of the experiments (described below). Biomass is recorded as μg chlorophyll *a* cm^{-2} colonization surface. As an aid interpreting responses to nutrients under different light treatments, biomass was normalized to Total nutrient treatment responses so that Total is equal to 1. This is called LETSI in a lotic ecosystem trophic system index proposed by Matlock (1996).

Two-way ANOVAs were run for each experiment on the chlorophyll *a* and chlorophyll *c:a* ratios. Pairwise multiple comparisons (Student-Newman-Keuls method) were performed to determine significant differences in responses to nutrient and light treatments and nutrient x light interactions. All tests were at the 95% confidence level using SigmaStat 1.0 for Windows.

Experimental Plan and Mesocosm Conditions

Pilot

A pilot study was conducted for two weeks ending 7 November 1994. The six nutrient solutions were replicated 18 times for a total of 108 periphytometers. There were no light-attenuating treatments. The water was turbid with 11 to 18 mg sediment liter^{-1}, and light at 30 cm depth was 35-45% of incident light. Flow velocity was 1 cm sec^{-1} and flow rate was 3.1 l sec^{-1}. The 4 liter periphytometers were left in the flume 2 weeks, with the colonizing surfaces 5 cm under the surface.

Spectrophotometry yielded optical density (OD) values at 664 nm (chlorophyll *a*) between 0.1 and 1.0 as recommended by APHA (1989). Using the algorith supplied in the method (APHA, 1989), I converted OD values (Appendix D) to biomass as chlorophylls *a, b*, and *c*. Kruskal-Wallis one way ANOVA on ranks showed a statistically significant difference ($p < 0.0001$) in the median values of chlorophyll *a* response to nutrients (Fig. 3). Nutrient solutions with combined nitrogen and phosphorus (N+P and Total) stimulated highest growth, indicating they were co-limiting nutrients for periphyton growth in the mesocosm,and were not statistically different from each other. After an ANOVA on pilot chlorophyll *a* with SAS®, a random deletion of replicate data showed that at least five replicates would be required to maintain statistical validity at the 95% confidence level (personal communication, M. Payton, Assistant Professor, Oklahoma State University Statistics Department, Stillwater, OK, 1994). Based on the results of

this bootstrap statistical operation on pilot data, six replicates were assumed adequate for further studies.

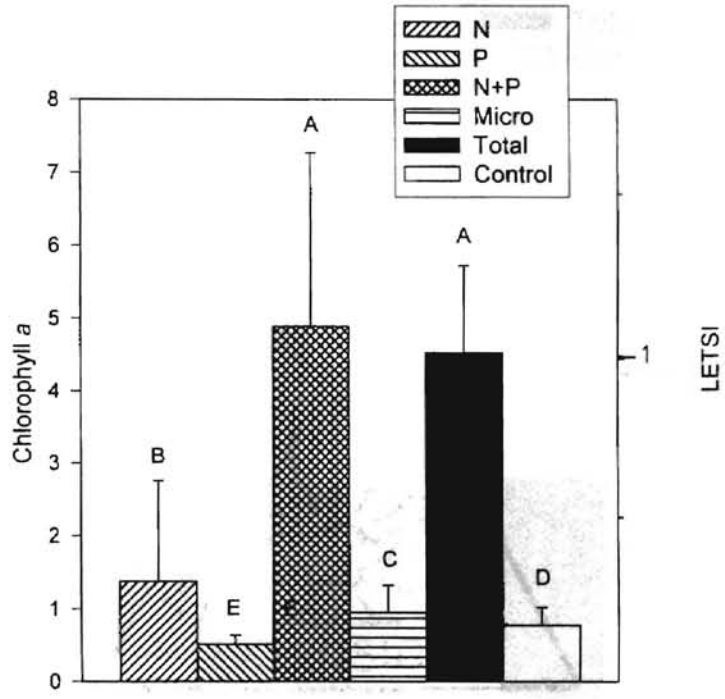

Figure 3. Pilot chlorophyll *a* ($\mu g\ cm^{-2}$) biomass response to nutrients, absolute and LETSI (mean ± SE; n=18). Bars with the same letter are not significantly different.

Figure 4 shows chlorophyll *c:a* ratio responses to the nutrient solutions. Higher *c:a* ratio means more diatoms relative to other taxonomic groups. Even though there were statistically significant differences (α=0.05) in chlorophyll *c:a* ratio responses to nutrients, except between N+P and Total, all ratios indicate dominance by diatoms. The relatively greater proportion of chlorophyll *a* may indicate presence of cyanobacteria and/or green algae on filters collected from N+P and Total.

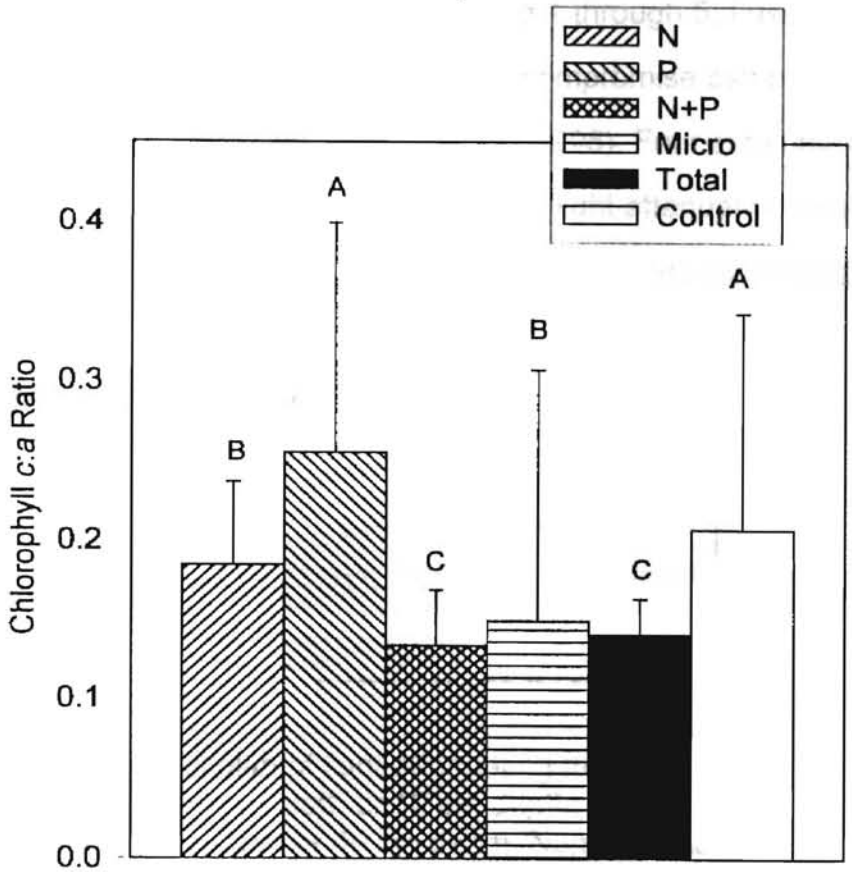

Figure 4. Pilot chlorophyll *c:a* ratio responses to nutrients (mean ± SE; n=18). Bars with the same letter are not significantly different.

The intent of the subsequent series of experiments was to compare algal responses to nutrients under identical flow regimes but different sediment levels. At first a sandfilter, built according to plans by Roberts and O'Hern (1993) with crushed anthracite added as a filtering aid, failed to sufficiently retain the colloidal-size clay particles, then a seep well failed to provide adequate water volume. Hazardous waste disposal and time and space concerns precluded the possibility of chemical flocculation and settling at the site. Flow rate varied with attempts to manipulate sediment levels but was constant throughout each experiment.

For the remaining experiments, numbered 1 through 5, I used 1 liter cubitainers. The reduction in volume did not compromise osmotic differential of nutrient ions across the membrane (Matlock, 1996). Four experiments used shade, and a fifth used depth, to provide three light attenuation treatments in each experiment. Each nutrient treatment was replicated six times per light treatment, three in each of two blocks. Figure 5 repesents the factorial distribution of treatments in the flume.

	L2	L1	L3
siphon	123456 421365 631542	351426 213465 315642	523614 234156 246135

Figure 5. Experimental plan of light attenuating treatments. Depending on the experiment, L1 = 0% shadecloth or 10 cm depth; L2 = 30% shadecloth or 25 cm depth; L2 = 63% shadecloth or 40 cm depth. Numbers indicate nutrient solutions. Half the flume is represented, i.e., the three light treatments (L1-L3) were duplicated.

Experiment #1 (7 days ending 21 June 1995)

Ambient nitrate concentration was 1.6 to 1.8 mg l^{-1}, phosphate was 0.09 to 0.1 mg l^{-1}. Turbidity measured 27 to 38 NTU. Black horticultural shade cloths with shade designations of 30 and 63% were used to establish three relative light levels at the water surface of 100% (no shade), 70, and 37%, respectively. The periphytometer colonization surfaces were 40 cm below the surface. Water temperature was 26 to 28 °C at midday. Water had a velocity of 1 cm sec^{-1} and flow volume of 3.1 l sec^{-1}.

Experiment #2 (7 days ending 3 July 1995)

Nitrate was 0.5 to 1.0 mg l^{-1}, phosphate 0.01 to 0.02 mg l^{-1}. The 2-m deep seep well dug between the dam and mesocosm produced water with a turbidity of 4 mg l^{-1} and 4.4 NTU. The supply did not adequately exceed evaporation loss, however, so the result was an overall depth of 15 cm with colonization surfaces 10 cm below the surface and no measurable flow. Temperature was 31 to 34 °C. As in Experiment #1, the shade cloths were used.

Experiments #3 and 4 (7 days each ending 14 and 23 July 1995)

Nitrate measured 1.3 to 2.3 mg l^{-1}, phosphate 0.05 mg l^{-1}. For these experiments I used well water plus enough siphoned lake water to provide a flow of 0.4 l sec^{-1} and turbidity of 10 to 18 mg l^{-1} and 12 to 20 NTU. The colonization surfaces were 40 cm below the surface. Temperature was 29 to 33 °C. Shade cloths were again used.

Experiment #5 (9 days ending 8 August 1995)

Nutrient concentrations were similar to the preceding experiments. Nitrate was 1.2 to 1.7 mg l^{-1}, phosphate 0.04 to 0.06 mg l^{-1}. Flow was returned to 3.1 l s^{-1} with lake water which increased turbidity to 16 to 21 mg l^{-1} and 15 to 22 NTU. In place of shade cloths, different heights provided light attenuation using ambient suspended sediment. The colonization surfaces were 10, 25, and 40 cm below the water surface. Relative sunlight at each depth was 95%, 75%, and 45% of surface light, respectively. Temperature was 30 to 31 °C. Table II

summarizes the physical and chemical measurements of the flume for the pilot and subsequent experiments.

Table II. Physical and chemical conditions of flume for pilot and experiments. Values are for measurements taken at beginning and end of experiments.

experiment	sediment (mg l^{-1})	NTU	flow (l sec^{-1})	time (days)	depth (cm)	temp (°C)	NO_3 (mg l^{-1})	PO_4 (mg l^{-1})
Pilot	18, 11	--	3.1	14	5	20, 19	--	--
#1	19, 30	27, 38	3.1	7	40	24, 25	1.6, 1.8	0.09, 0.10
#2	4, 4	4.4, 4.4	0.0	7	10	30, 34	1.0, 0.5	0.02, 0.01
#3	18, 14	20, 16	0.4	7	40	29, 30	1.5, 2.3	0.05, 0.05
#4	10, 15	12, 19	0.4	7	40	30, 33	1.3, 1.9	0.05, 0.05
#5	16, 21	15, 22	3.1	9	10, 25, 40	30, 31	1.2, 1.7	0.04, 0.06

CHAPTER IV

RESULTS

Plankton and Periphyton Identification

Plankton estimates from lake water entering the flume via siphon from 6 m below the surface from July through November 1994 varied from 22 to 61 organisms ml^{-1}, predominantly *Melosira* (Appendix A). Zooplankton were not present.

Periphyton assemblages varied according to substrate and were more diverse than the plankton (Appendix B). The dominant class was diatoms, primarily small pennates epiphytic on *Cladophora*. Consumers were present. It appeared a healthy inoculum was available for the periphytometers.

Filters from Matlock periphytometers collected June 6 after 12 days in the flume had both algae and invertebrates (Appendix C). There were visible differences in greenness between nutrient treatments. N+P and Total had the most growth; Control had the least growth.

Diatoms was generally the most abundant algal class in each sampling event, from phytoplankton to periphytometers, but they were not epiphytic on *Cladophora* on the periphytometer filters.

Experiment #1

Turbid water with shade cloths produced maximum average chlorophyll biomass of less than 1 $\mu g\ cm^{-2}$ (Fig. 6). The greatest response was to Micro, with Total a distant second. The greatest overall biomass response was recorded at the 70% relative light level. Main effects of nutrient and light were significant ($p<0.0001$). Micro was significantly different from every other nutrient treatment at the 100 and 70% light levels. Responses to all other nutrient treatments were not significantly different. The only significant differences between responses to light treatments were between 70 and 37% light and 100 and 37% light. There was not a statistically significant light x nutrient interaction.

Experiment #2

The no-flow condition in Experiment #2 increased temperatures and reduced transport of inoculum propagules to the periphytometers. Instead, floating mats of algae covered much of the water. These were primarily *Spirogyra* and *Cladophora*, while periphyton found on the colonization sites in flow situations consisted primarily of diatoms. The maximum average chlorophyll biomass was less than 0.2 $\mu g\ cm^{-2}$. The N+P and Total nutrient and 70% light treatments resulted in the highest response. When biomass estimates were normalized to Total mean, responses to N+P declined with light reduction (Fig. 7). Both nutrients ($p<0.0001$) and light ($p=0.0018$), but not nutrient x light interaction, significantly affected biomass accumulation. Total at the 70% light level was different from all other nutrients. There were no other significant differences in responses to nutrients. There were significantly different biomass responses to

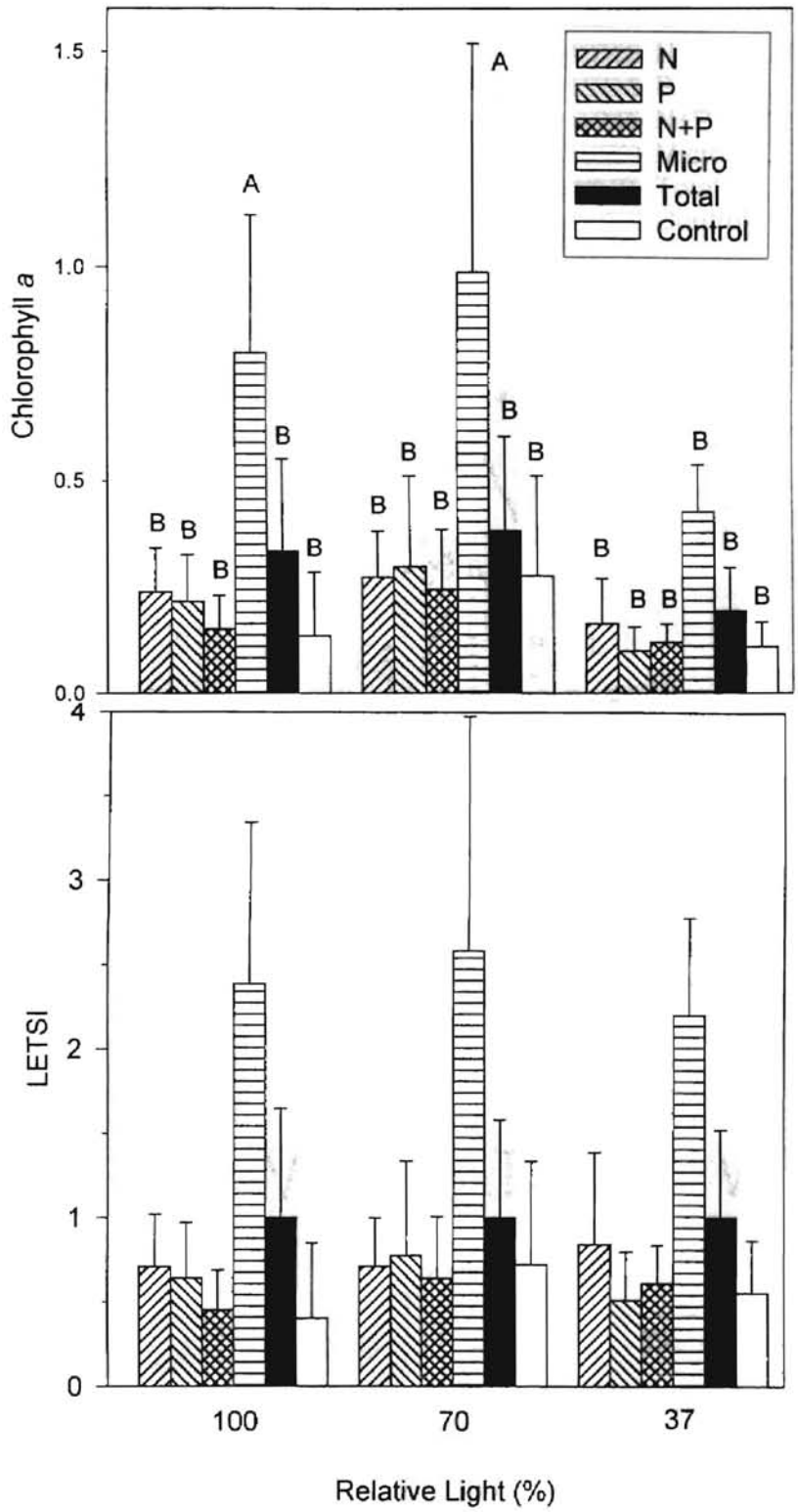

Figure 6. Experiment #1 chlorophyll *a* ($\mu g\ cm^{-2}$) biomass responses to nutrients and light, absolute and LETSI (mean ± SE; n=6). Bars with the same letter are not significantly different.

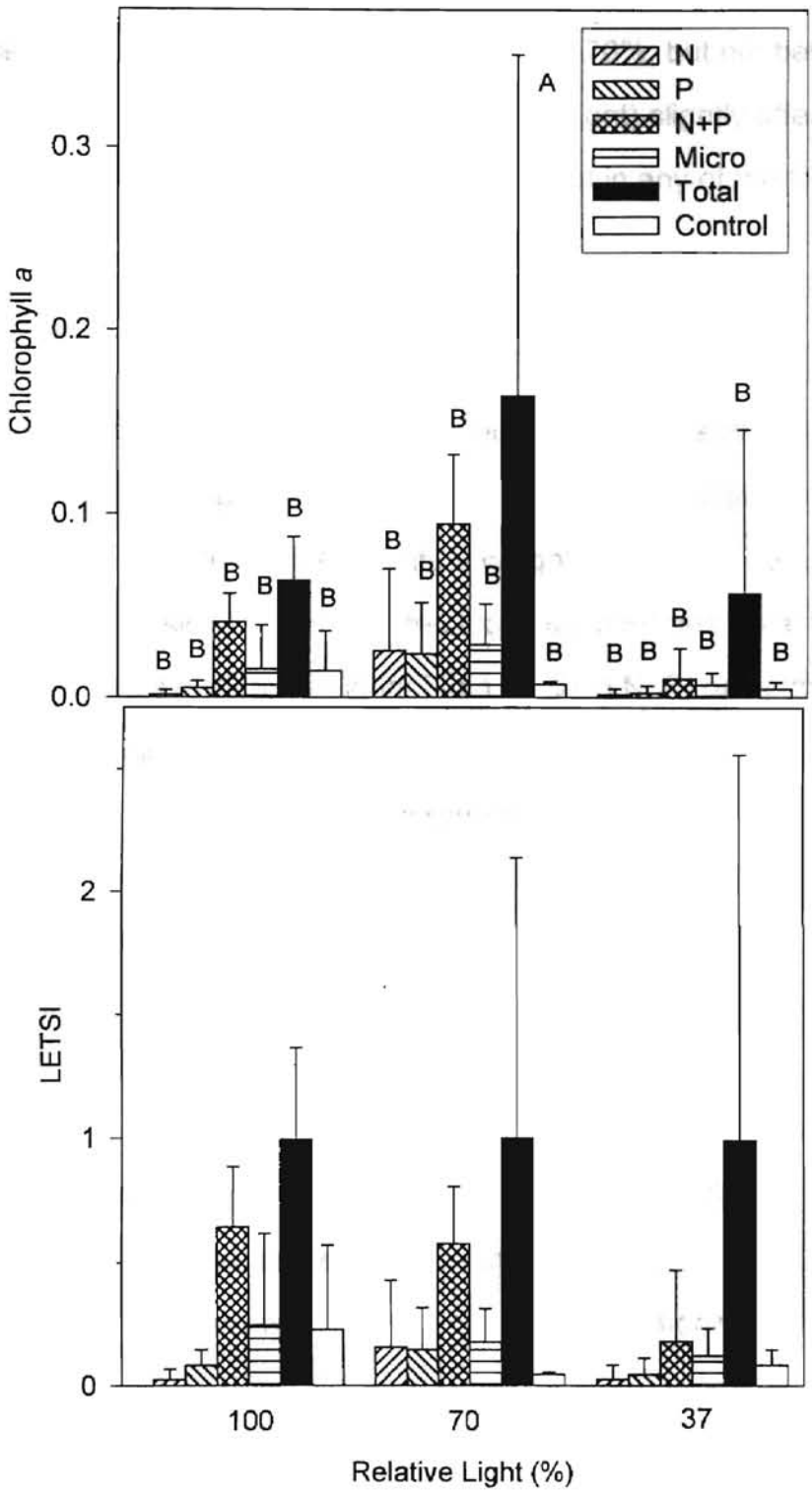

Figure 7. Experiment #2 chlorophyll *a* ($\mu g \cdot cm^{-2}$) biomass response to nutrients and light, absolute and LETSI (mean ± SE; n=6). Bars with the same letter are not significantly different.

light levels between 100 and 70% and 37 and 70%, but not between 37 and 100%. Nutrients (N at 37 and Control at 70% light) slightly affected chlorophyll *c*:*a* ratios ($p=0.0433$; not shown) in this, but not in any of the following experiments.

Experiment #3

The maximum average chlorophyll biomass was less than 0.3 $\mu g\ cm^{-2}$. N+P and Total nutrient regimes and 70% light treatments resulted in the highest biomass response (Fig. 8). Nutrients and light (both $p<0.0001$), but not nutrient x light interaction, significantly affected biomass. N+P and Total nutrient treatments had significantly higher biomass than N, P, or Control, but only at 70% relative light.

Experiment #4

The maximum average chlorophyll biomass was less than 0.3 $\mu g\ cm^{-2}$. Nearly half of the 30% shaded periphytometer filters were at least partly gone - possibly due to macroinvertebrate activity. Even so, the highest biomass occurred at the 70% relative light level (Fig. 9). Unlike all other experiments, light ($p<0.0001$), but not nutrients ($p=0.6994$) significantly affected biomass. Significant differences occurred between 100 and 70% and 70 and 37% light levels, but not 100 and 37%. Light x nutrient interaction was not significant ($p=0.38$).

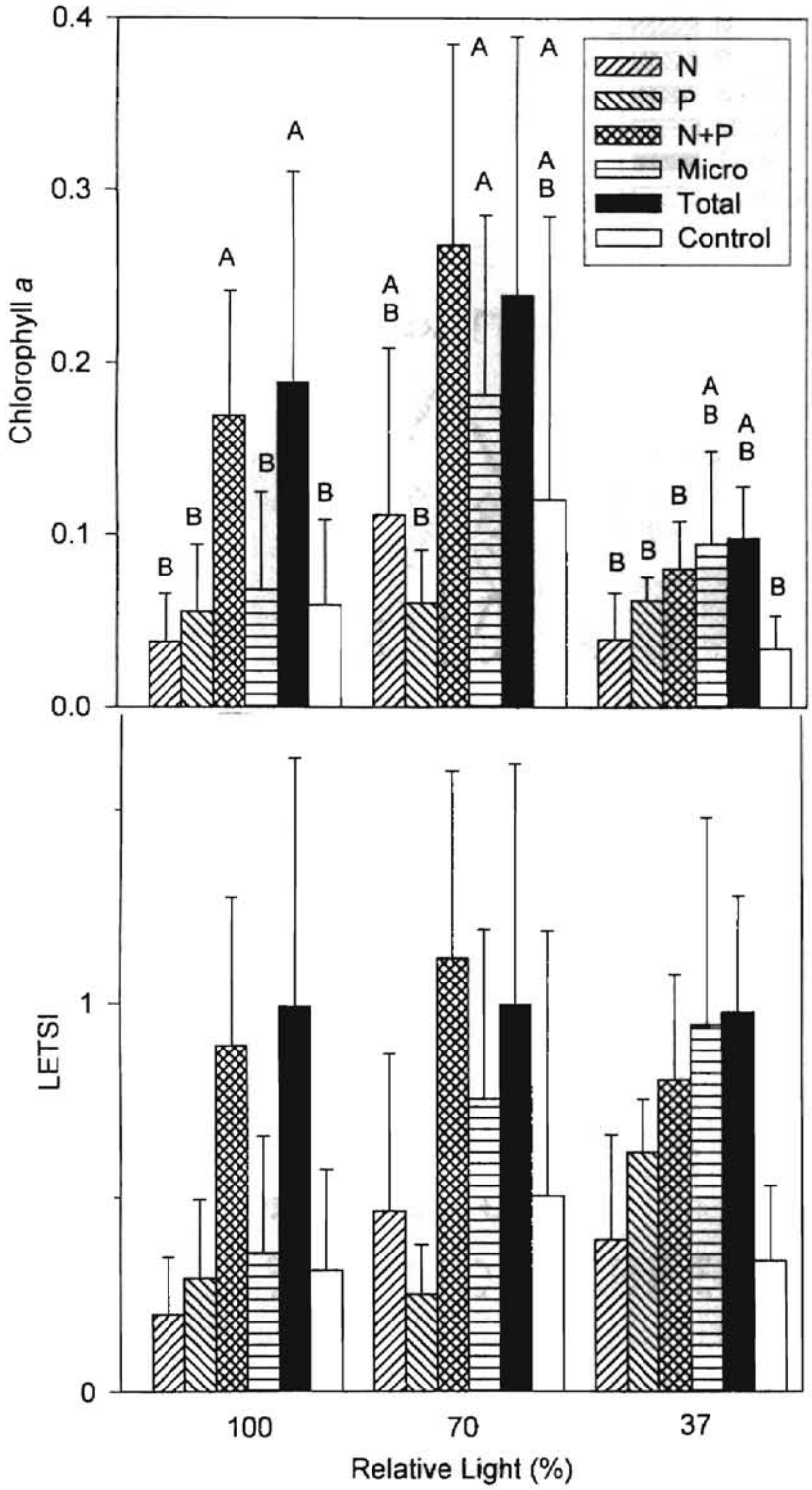

Figure 8. Experiment #3 chlorophyll *a* ($\mu g\ cm^{-2}$) biomass responses to nutrients and light levels, absolute and LETSI (mean ± SE; n=6). Bars with the same letter are not significantly different.

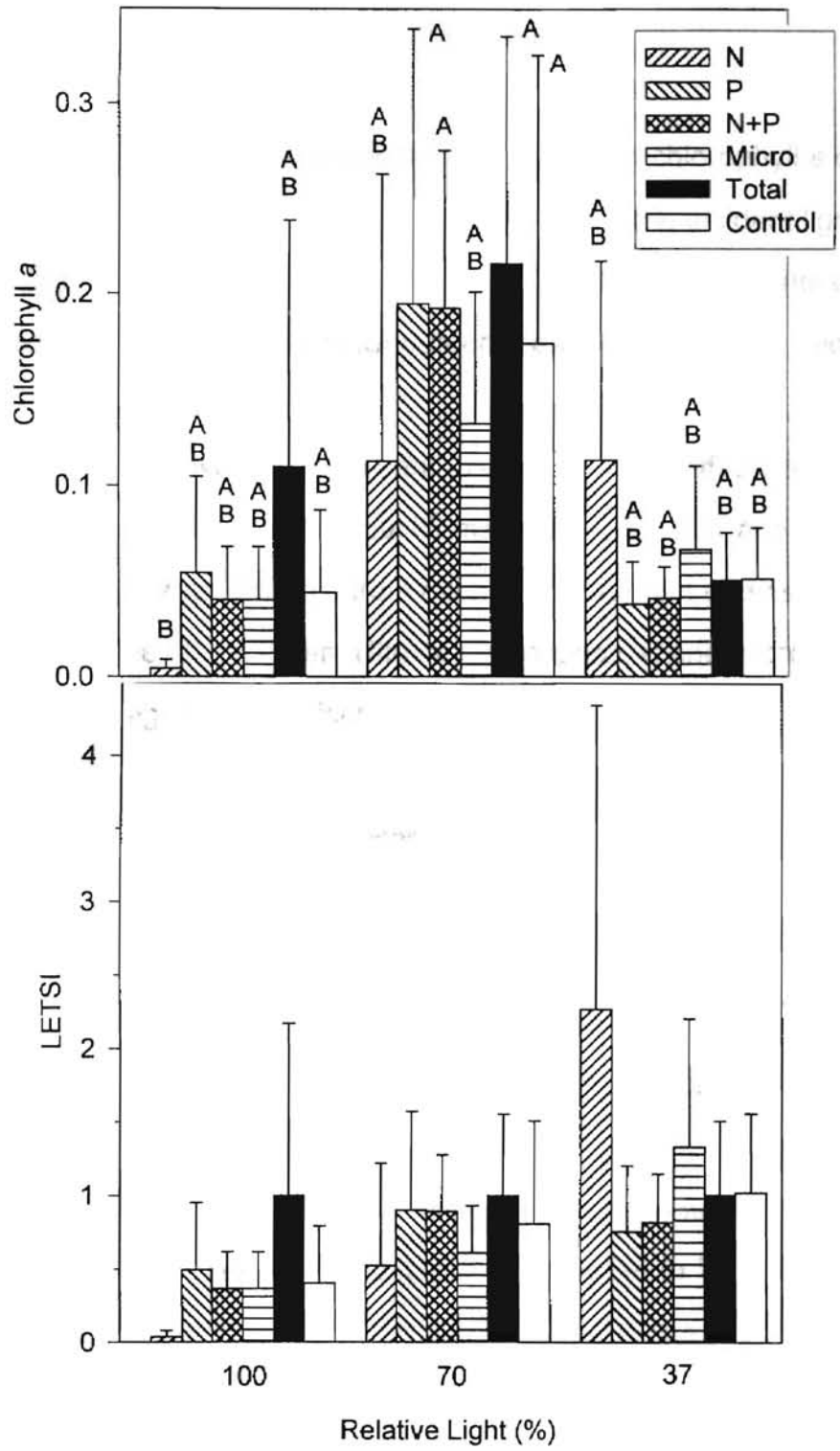

Figure 9. Experiment #4 chlorophyll *a* ($\mu g \cdot cm^{-2}$) biomass responses to nutrients and light, absolute and LETSI (mean ± SE; n=6). Bars with the same letter are not significantly different.

Experiment #5

Maximum average biomass was more than 2 μg chlorophyll *a* cm^{-2}. Ten, 25, and 40 cm depths were equivalent to 95, 75, and 45% incident light, respectively. N+P and Total nutrient and 10 cm depth treatments enhanced algal biomass similarly relative to other nutrient treatments (Fig. 10). Biomass decreased with decreasing light.

Experiment 5 revealed significant ($p<0.0001$) main effects and interaction of light (depth) and nutrients on algal biomass. Effects of 25- and 40-cm depths were not significantly different from each other. Nutrient effects were not significant at the 40 cm depth. Nitrogen, phosphorus, and micronutrients added alone did not significantly affect biomass at any depth.

Results Summary

A trend of greater biomass response to micronutrients relative to combined macronutrients (N+P and Total) with reduced light was observed in several comparisons. For instance, Experiment #1 had the highest turbidity and the highest response to micronutrients of all experiments. Experiment #2 had almost no turbidity, and the importance of micronutrients to algae in decreasing light was revealed in decreased response to N+P relative to Total. The pattern of responses to all nutrients in #2 was similar to that of the pilot, where the periphytometers experienced minimal light attenuation due to their proximity to the surface. Experiments #3 and #4 showed a significant trend toward increased response to Micro relative to Total with decreasing light. The trend seen in #5 was not significant at the 0.05 level of probability.

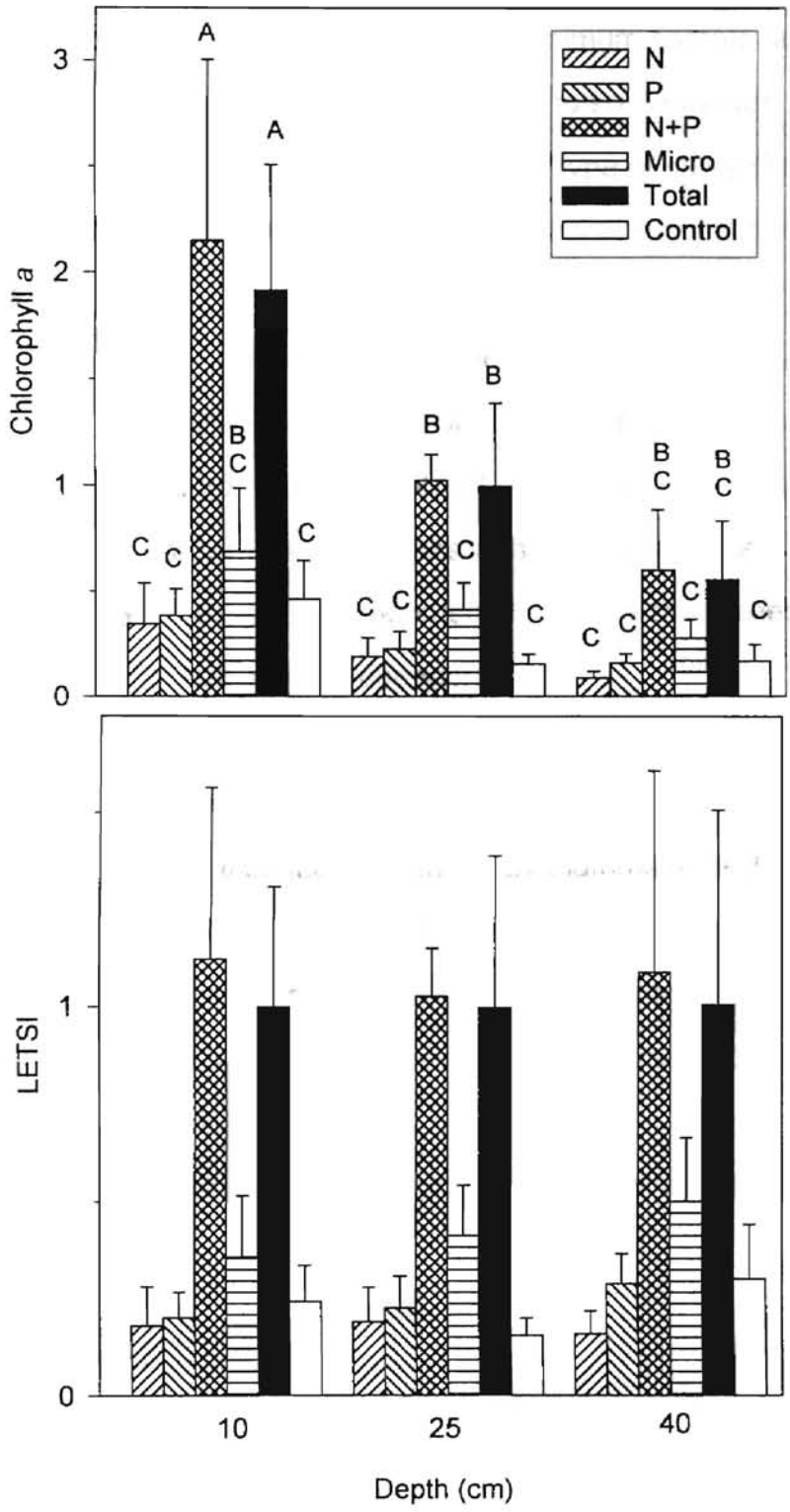

Figure 10. Experiment #5 chlorophyll *a* ($\mu g \cdot cm^{-2}$) biomass response to nutrients and depth, absolute and LETSI (mean ± SE; n=6). Bars with the same letter are not significantly different.

A more formal method for determining minimum sample number (Ott, 1993) from pilot data indicated nine was preferable to six. However, less stringent statistical parameters are appropriate for this type of study (Krebs, 1989). A confidence level of 80 or 90% would yield more significant differences between treatments.

The biomass responses in Experiment #5 produced optical densities at 664 nm (chlorophyll *a*) between 0.1 - 1.0 optical density (OD) as recommended by APHA (1989). ODs from Experiments #1, 2, 3, and 4 were marginally adequate, generally between 0.01 - 0.1. Biomass was generally highest in N+P and Total nutrient treatments except in Experiment #1, where the highest ODs, averaging 0.09, were in Micro samples (Appendix D).

The extremely low chlorophyll *b* in all my periphytometer samples (Appendix D) shows that Chlorophytes were present in very low numbers, if at all. The chlorophyll *c:a* ratios indicate dominance by diatoms regardless of light or nutrient levels. Lower *c:a* ratios in samples with higher biomass from N+P or Total treatments denoted presence of Cyanobacteria and/or Chlorophytes. Statistical significance of differences among *c:a* ratios at the 95% confidence level was not biologically significant.

Appendix E summarizes statistics for chlorophyll *a* biomass in the pilot and Experiments #1-5.

CHAPTER V

DISCUSSION

Plankton and Periphyton Identification

Dominance by diatoms can be expected because of the low nutrient levels in the lake and flume water. It follows that chlorophyll *c:a* ratios would fall in or very near to diatom range of 0.2 - 0.5 for each nutrient treatment if the available propagules are primarily diatoms. Cyanobacteria and green algae were present, but not dominant, as seen in microscopic examination of plankton, periphyton and periphytometers, and in chlorophyll *c:a* ratios.

Chemical, Physical, Biological, and Method Considerations

Chemical

How suspended sediments affect biomass and/or chlorophyll ratios may depend on the chemistry of the clay and how well it competes with the algae in nutrient scavenging. In Lake Carl Blackwell, the predominant clay is montmorillonite, a plastic, cohesive, colloidal clay with a high cation exchange capacity. It was anticipated that the clay might interfere with algal colonization of the periphytometer by attraction to and clogging of the diffusing substrate, especially at low flow rates. This did not happen at any flow rate or turbidity level.

However, in the Micro periphytometers of some of the experiments, a brown film appeared between the filter and membrane. This was perhaps iron precipitating out of solution due to the high solute concentration and pH (7.5 - 8.5) of the flume water. Another possible explanation is that tiny clay particles passed through the filter in the anticipated chemical attraction.

In the pilot, some of the Total solution formed a white precipitate inside the reservoir after 3 days. I did not see this in later experiments where the periphytometers were exposed to less light and/or higher temperatures.

Physical

The clay did not interfere with algal colonization of the periphytometer by clogging of the diffusing substrate, even at the slowest flow rates in Experiments #3 and 4. This was probably achieved by the vertical, and parallel to streamflow, orientation of the colonizing surface. Logistics eliminated the possibility of examining effects of various concentrations or types of sediment.

Season may play a role in biomass and species composition, i. e. chlorophyll *c:a* ratios. Higher ultraviolet radiation (such as in summer) has been shown to decrease lotic periphytic diatom community growth in the first few weeks, increase growth after 5 weeks, and change species composition over longer periods (Bothwell et. al., 1993). Nutrient-deficient algae have been shown to be especially sensitive to UV radiation (Lesser et. al, 1994). Biomass accumulation may be lower in spring and fall than in winter (Matlock, 1996). Napolitano (1994) suggests measuring sterols instead of chlorophyll to estimate biomass because he found chlorophyll cell content to vary with light.

Location attributes such as ambient nutrient levels or canopy might affect the duration of deployment. Since the pilot (14 days) and Experiment #5 (9 days) had the highest biomass, I might conclude that 7 days (Experiments #1-4) is too short to accumulate reliably measurable biomass in the nutrient-poor mesocosm. However, variations occurred in sediment, light, flow, season, and temperature, each of which could affect biomass accumulation and taxonomic composition (Oemke and Burton, 1986). The periphyton in Experiment #2, with its lack of turbidity and proximity of periphytometers to the surface, may have been light inhibited. Flow may have been insufficient to supply propagules to the colonization surfaces. Aloi (1990) states that the consensus for exposure period of artificial substrates indicates a minimum of 1 month.

Biological

Decomposition of membranes tended to occur after about one week in periphytometers without penicillin, especially in N+P and Total nutrient treatments. In addition to other bacteria, Penicillin G inhibits some Cyanobacteria (*Anabaena variabilis, Microcystis aeruginosa*) growth at concentrations of 2 ppm or less and the Chlorophytes *Chlorella pyrenoidosa* and *Scenedesmus obliquus* at 1000 ppm (Lewin, 1962). The penicillin mode of action is to prevent peptidoglycan cell wall synthesis of Gram positive bacteria (Tortora, et. al., 1992). It is not supposed to be clinically effective against Gram-negative bacteria. Cyanobacteria are Gram-negative, and some have a polysaccharide sheath protecting them from such antibiotics (Staley et. al., 1989). Penicillin G procaine and penicillin G benzathine have molecular weights of 570.71 and 909.11, respectively (Windholz, 1983). These molecules are larger than the

nutrient molecules but still considerably smaller than the periphytometer dialysis membrane with molecular weight cutoff of 12000. The Merck Index (Windholz, 1983) states penicillin G procaine is not affected by light, but makes no statement for other penicillin G's. Penicillin was not used in nutrient solutions in the pilot, which had a chlorophyll *b* response as well as overall greater biomass, or for periphytometer periphyton identification where Chlorophytes were seen.

Few significant differences were revealed in *c:a* ratios because the propagules are mainly diatoms, which respond similarly to changes in light conditions (adaptations, ie changing pigment ratios by a single taxon to different light levels). Also, the very low biomass created difficulty in accurately measuring ratios using the spectrophotometric trichromatic method. Other accessory pigments have been used with HPLC to determine taxonomic differences in algal communities as trophic status indicators (Claustre, 1994).

The extremely low chlorophyll *b* in all my periphytometer samples shows that green algae are present in very low numbers. The chlorophyll *c:a* ratios indicate a dominance by diatoms, with some presence of Cyanobacteria and/or Chlorophytes in some samples, regardless of light or nutrient levels. Even when statistical analysis indicated a significant difference in ratios at the 95% confidence level, a biological significance could not be seen because the ratios were within the literature values for diatoms. The data obtained in these experiments did not support the use of pigment ratios obtained from the periphytometers use as a sediment- and nutrient- indicating biomonitor.

Methods

Even though Experiments #1-4 (shade cloths) showed highest biomass at 70% light, light-inhibition of unshaded periphytometers is an unlikely explanation when depth and ambient turbidity are considered. Increased grazing on the unshaded periphytometers is a possible explanation. Grazing was an unknown variable in the mesocosm experiments. Matlock (1996) controlled grazing in some field experiments by screening the colonization surfaces with aluminum mesh. Sometimes the screens collected material which prevented light from reaching the colonization surfaces. Aloi (1990) refers to 'current', but unspecified, tests involving nutrient- and insecticide-diffusing substrates. This may be a less troublesome way of eliminating grazing variability in canopy experiments if regulations regarding pesticides in water can be satisfied.

The spectrophotometric method may not be the most valid method of chlorophyll determination where biomass is low (whether due to low nutrients or high turbidity). Shaking the samples instead of grinding saved time but possibly resulted in incomplete chlorophyll extraction. However, DeNicola and Hoagland (1992) shook their natural sand- and gravel- substrate samples during the extraction process. Their mean chlorophyll values ranged from 0.54 to 3.26 μg cm^{-1} (similar to this study), depending on substrate and canopy openness. In some studies involving chlorophyll extraction from periphyton, samples were homogenized in a blender (Biggs, 1995), rather than ground which would probably more thoroughly break the cells for pigment extraction. Schneider et. al. (1995) extracted periphyton directly in dimethylsulfoxide (DMSO) without removing the samples from the substrate. Marker et. al. (1980) reported that acetone, without grinding, readily extracts pigments from diatoms, the dominant

class of algae in my mesocosm. Although grinding was specified in the method used (APHA, 1989), I can not conclude whether shaking the samples did or did not adequately extract chlorophyll in these experiments. Considering the results of the study as a whole, the low biomass in most of the experiments is easily attributed to low ambient nutrients and propagule numbers, extreme turbidity or light inhibition, and short colonization period.

In some samples, centrifuging did not pellet the fibers well enough to prevent interference in spectrophotometer readings even though great care was taken when pipetting the supernatant. In a discussion of phytoplankton pigment analysis, Marker et. al. (1980) recommended Whatman GF/C glass fiber filters (GFF) rather than membrane filters because the GFF do not cause turbudity on centrifugation. They did not compare 934-AH GFF. Possibly, the finer GF/C or ground 934-AH would centrifuge better.

Determination of chlorophyll *c:a* ratios is dependent on trichromatic method calculations (APHA, 1989) which, at extremely low biomass such as in Experiments #1-4, can result in negative numbers, an impossibility. Marker et. al. (1980) advise against use of the trichromatic method because of their lack of confidence in accuracy of the equations.

The fluorometric method is a more sensitive method of chlorophyll analysis at low concentrations and is fairly simple to execute, but it does not allow identification of separate chlorophylls (APHA, 1989). High performance liquid chromatography (HPLC) does permit identification of separate chlorophylls (APHA, 1989). Niederhauser and Schanz (1993) used HPLC to obtain chlorophyll *b:c* ratios. Their data indicated dominance by diatoms in nutrient-diffusing flower pots with nitrogen (N), phosphorus (P), and carbon (C) treatments, but increased green algae response, as indicated by higher *b:c* rato,

to nutrient solutions containing phosphorus. HPLC, however, is not as simple to execute as spectrophotometry or fluorometry and is unavailable in many laboratories.

The purpose of nutrient-diffusing periphytometers is to identify limiting nutrients in a stream or lake. Agar-based nutrient-diffusing clay periphytometers are similar to the Matlock periphytometer in having a constant diffusion rate for at least 3 weeks (Aloi, 1990; Matlock, 1996). Cattaneo and Roberge (1991) reported sample losses of greater than 50% when using brushing and scraping as opposed to direct extraction of chlorophyll from the substrate. They also found that increased flow reduced sampling efficiency. The ability to quickly and completely harvest the periphyton is the main advantage of the nutrient-diffusing periphytometric system used in this study.

The range of periphyton chlorophyll *a* biomass means measured on the mesocosm periphytometers from Experiment #5 (0.5 - 2.3 $\mu g\ cm^{-2}$) is similar to those reported by Matlock (1996) and Pringle et. al. (1986). Niederhauser and Schanz (1993) reported a maximum biomass of 12.9 $\mu g\ cm^{-2}$ from combined N-, P-, and C-diffusing clay pots, indicating a co-limited situation, and a minimum of 0.47 $\mu g\ cm^{-2}$ on controls after 42 days in an oligotrophic lake. Longer colonization periods would have resulted in greater biomass accumuation in the mesocosm experiments. Therefore, this study supports use of the Matlock periphytometer as a method for estimating biomass.

Conclusions

These experiments show that suspended sediments affect biomass responses to nutrients. The main effect seen here is light attenuation which

reduces growth. Light attenuation sometimes altered responses to nutrients but not in every experiment. Extreme attenuation, whether caused by shade cloth, sediment, or depth in turbid water, also reduces the differences between responses to different nutrients. A more relaxed confidence limit (Matlock, 1996, used 80% in his field experiments) could have shown more significant results.

Conclusions drawn from chlorophyll data support previous characterizations of Lake Carl Blackwell as turbid and nutrient-poor using other methods (Faust, 1973; Howick and Wilhm, 1985; Muoneke et. al., 1992; Nolen et. al., 1985; Schrieber, 1958; and Spall, 1968). Biomass responses to nutrients under different light levels indicate that the mesocosm was co-limited by nitrogen, phosphorus, and light.

This study indicates that the value of the Matlock periphytometer for assessing nutrient limitation may be influenced by light, as are other nutrient-diffusing periphytometers. I was not able to address whether a standard depth from the surface will suffice when sediment-derived turbidity or incident light varies widely between sites.

Hypotheses Decisions

I have sufficient data to conclude that nutrients, light, and nutrient x light interactions significantly affect biomass accumulation by periphytometers, measured as chlorophyll *a*. Therefore, I reject the null hypotheses 1, 3, and 5.

I do not have sufficient data to conclude that nutrients, light, and nutrient x light interactions significantly affect chlorophyll *c*:*a* ratios measured in algae colonizing nutrient-diffusing periphytometers. Therefore, I fail to reject the null hypotheses 2, 4, and 6.

Recommendations for Future Research

I was frustrated by the inability to control sediment levels in the mesocosm because of my water source. The site did not permit settling or chemical floculation, and filtering was not possible due to the particle size, concentration of sediment, and volume of water required. The seep well did not provide enough volume. I would suggest doing the study in a clear non-chlorinated water location, i. e., well or diverted stream, to allow sediment or other light manipulation as follows:

1) Add different types of sediment in order to compare effects of montmorillonite and kaolinite, for instance.

2) Compare effects of light attenuation caused by different amounts of sediment.

3) Compare effects of light attenuation caused by shade vs sediment. Some variations in shade could include canopy height or light quality.

4) Manipulate flow rates to determine the range for optimum periphyton growth under various sediment levels.

5) Manipulate nutrient concentrations in the mesocosm in addition to the nutrient-diffusing periphytometers, so that the algal community available for propagules can be more diverse.

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APPENDICES

Appendix A

Phytoplankton Identification and Abundance

Date and Location	Number/ml	Genus (**boldface** most abundant)	Order	Class
13 July 94 lake by dock	61	***Melosira***	Centrales	Bacillariophyceae
		Cymbella	Pennales	Bacillariophyceae
		diatoms	Pennales	Bacillariophyceae
		Anabaena	Nostocales	Cyanophyceae
		Trachelomonas	Euglenales	Euglenophyceae
		Trochiscia	Chlorococcales	Chlorophyceae
		Cosmarium	Zygnematales	Chlorophyceae
		unknown groups of tiny cells		Chlorophyceae or Cyanophyceae
9 July 94 lake by dam	39	***Melosira***	Centrales	Bacillariophyceae
		diatoms	Pennales	Bacillariophyceae
		Trachelomonas	Euglenales	Euglenophyceae
		Anabaena	Nostocales	Cyanophyceae
		unknown groups of tiny cells		Chlorophyceae or Cyanophyceae
3 Aug 94 siphon	22	***Melosira***	Centrales	Bacillariophyceae
		unknown groups of tiny cells		Chlorophyceae or Cyanophyceae
		Ceratium	Dinokontae	Dinophyceaea
		Trochiscia	Chlorococcales	Chlorophyceae
16 Aug 94 flume	50	***Melosira***	Centrales	Bacillariophyceae
		unknown groups of tiny cells		Chlorophyceae or Cyanophyceae
18 Aug 94 flume	52	***Melosira***	Centrales	Bacillariophyceae
		unknown groups of tiny cells		Chlorophyceae or Cyanophyceae
26 Aug 94 flume	37	***Melosira***	Centrales	Bacillariophyceae
		unknown groups of tiny cells		Chlorophyceae or Cyanophyceae
15 and 29 Sep 94 flume	28	***Melosira***	Centrales	Bacillariophyceae
		unknown groups of tiny cells		Chlorophyceae or Cyanophyceae
5 Oct 94 flume	23	***Melosira***	Centrales	Bacillariophyceae
		Cymbella	Pennales	Bacillariophyceae
		unknown groups of tiny cells		Chlorophyceae or Cyanophyceae
24 Oct 94 flume	not quantified	***Melosira***	Centrales	Bacillariophyceae
		unknown groups of tiny cells		Chlorophyceae or Cyanophyceae
		Cymbella	Pennales	Bacillariophyceae
		Fragilaria	Centrales	Bacillariophyceae

Appendix B

Periphyton Identification

Date and Location	Genus (**boldface** most abundant)	Order	Class
13 July 94 lake by dock	***Spirogyra*** and diatoms*	Zygnematales Pennales	Chlorophyceae Bacillariophyceae
17 Aug 94 lake by dam	***Cladophora*** and diatoms	Siphonocladales Pennales	Chlorophyceae Bacillariophyceae
	tiny dark bluegreen diatoms underside of rocks	Pennales	Bacillariophyceae
26 Aug 94 flume:	***Mougeotia***	Zygnematales	Chlorophyceae
30 Aug 94 flume	***Mougeotia***	Zygnematales	Chlorophyceae
	Oedegonium	Oedegoniales	Chlorophyceae
	Spirogyra	Zygnematales	Chlorophyceae
Microcrustacea were present among the periphyton.			
5 Oct 94 flume	***Spirogyra***	Zygnematales	Chlorophyceae
	Cymbella	Pennales	Bacillariophyceae
	Oedegonium	Oedegoniales	Chlorophyceae
	diatoms	Pennales	Bacillariophyceae
Crayfish, snails, insects present.			
24 Oct 94 flume	***Cladophora*** and diatoms	Siphonocladales Pennales	Chlorophyceae Bacillariophyceae
Crayfish, snails, insects present.			
3 Nov 94 inoculum rocks	***Cladophora***	Siphonocladales	Chlorophyceae
	Tabellaria	Centrales	Bacillariophyceae
Crayfish and snails present.			
3 Nov 94 flume wall	***Cladophora***	Siphonocladales	Chlorophyceae
	Spirogyra	Zygnematales	Chlorophyceae
	Tabellaria	Centrales	Bacillariophyceae
	Stigeoclonium	Chaetophorales	Chlorophyceae
	Ulothrix	Ulotrichales	Chlorophyceae
Snails present.			

17 May 95	***Cladophora***	Siphonocladales	Chlorophyceae
Inoculum rocks	and diatoms	Pennales	Bacillariophyceae
	Tabellaria	Centrales	Bacillariophyceae
	Rhoicosphenia	Pennales	Bacillariophyceae
	Melosira	Centrales	Bacillariophyceae
	Rhizosolenia	Centrales	Bacillariophyceae
	Closterium	Zygnematales	Chlorophyceae
	Ankistrodesmus	Chlorococcales	Chlorophyceae

Zooplankton, mostly rotiferans, were abundant, as were actively-feeding invertebrates: snails, dipterans (Chironomidae), amphipods and trichopteran larvae in web-like refugia.

17 May 95	***Cladophora***	Siphonocladales	Chlorophyceae
Flume wall	*Tabellaria*	Centrales	Bacillariophyceae
at surface	*Fragilaria*	Centrales	Bacillariophyceae

Invertebrates present.

17 May 95	***Fragilaria***	Centrales	Bacillariophyceae
Flume wall	*Oedegonium*	Oedegoniales	Chlorophyceae
at 30 cm	*Cymbella*	Pennales	Bacillariophyceae
	(sheathed chain and free)		
	Melosira	Centrales	Bacillariophyceae

Zooplankton were also present.

5 July 95	***Cladophora***	Siphonocladales	Chlorophyceae
Flume wall	*Rhoicosphenia*	Pennales	Bacillariophyceae
	Fragilaria	Centrales	Bacillariophyceae
	Spirogyra	Zygnematales	Chlorophyceae

5 July 95	***Spirogyra***	Zygnematales	Chlorophyceae
Floating masses:			

* 'and diatoms' refers to small epiphytes on filamentous algae

Appendix C

Periphytometer Periphyton Identification and Abundance, June 1995

Nutrient	Genus (**boldface** most abundant)	Order	Class
N	***Fragilaria***	Centrales	Bacillariophyceae
	Melosira	Centrales	Bacillariophyceae
	Platymonas, Carteria, or similar	Volvocales	Chlorophyceae
	unknown, small	Pennales	Bacillariophyceae
	unknown, masses of tiny cells	?	Chlorophyceae or Cyanophyceae
	Cymbella (in chains)	Pennales	Bacillariophyceae
	Closterium	Zygnematales	Chlorophyceae
	Cosmarium	Zygnematales	Chlorophyceae
	Bacillaria paradoxa	Pennales	Bacillariophyceae
	unknown	Ulotrichales	Chlorophyceae
	Stigeoclonium	Chaetophorales	Chlorophyceae
	Spirogyra	Zygnematales	Chlorophyceae
P	**same taxa as N,** similar abundance		
	more small flagellates	Volvocales	Chlorophyceae
	more cell masses	?	Chlorophyceae or Cyanophyceae
	Pediastrum	Zygnematales	Chlorophyceae
N+P	**same taxa as N** but more abundant overall than other treatments		
	Melosira varians	Centrales	Bacillariophyceae
Micro	**same taxa as N** except less abundant		
	more *Cosmarium*	Zygnematales	Chlorophyceae
	and *Cymbella*	Pennales	Bacillariophyceae
Total	**similar taxa as N+P,** similar abundance		
Control	**similar to N** but least abundant overall		
	relatively more diatoms	Pennales	Bacillariophyceae

Appendix D

Chlorophyll Optical Density Values

Pilot

treatment	750nm	664nm	647nm	630nm
N	0.003	0.128	0.035	0.031
N	0.003	0.089	0.026	0.022
N	0.004	0.092	0.027	0.024
N	0.002	0.128	0.036	0.031
N	0.003	0.121	0.035	0.031
N	0.015	0.160	0.057	0.050
N	0.025	0.133	0.049	0.045
N	0.002	0.228	0.059	0.055
N	0.006	0.116	0.035	0.031
N	0.003	0.182	0.054	0.055
N	0.006	0.078	0.032	0.025
N	0.009	0.115	0.039	0.033
N	0.003	0.090	0.025	0.021
N	0.020	0.110	0.053	0.050
N	0.012	0.154	0.051	0.046
N	0.003	0.086	0.026	0.023
N	0.007	0.759	0.208	0.192
N	0.010	0.132	0.044	0.040
P	0.018	0.064	0.033	0.031
P	0.003	0.076	0.022	0.017
P	0.003	0.032	0.013	0.011
P	0.007	0.078	0.029	0.028
P	0.084	0.131	0.100	0.099
P	0.063	0.108	0.085	0.087
P	0.025	0.095	0.047	0.044
P	0.007	0.076	0.026	0.023
P	0.011	0.089	0.032	0.028
P	0.021	0.077	0.038	0.034
P	0.015	0.067	0.032	0.028
P	0.017	0.082	0.036	0.033
P	0.008	0.083	0.029	0.025
P	0.018	0.065	0.033	0.031
P	0.039	0.098	0.061	0.055
P	0.042	0.094	0.064	0.064
P	0.018	0.066	0.035	0.032
P	0.041	0.094	0.062	0.060
N+P	0.007	0.337	0.110	0.079
N+P	0.008	1.231	0.349	0.285
N+P	0.003	0.587	0.176	0.129
N+P	0.037	0.866	0.301	0.226

N+P	0.017	0.839	0.274	0.189
N+P	0.014	0.792	0.259	0.184
N+P	0.010	0.303	0.103	0.073
N+P	0.006	0.749	0.239	0.167
N+P	0.020	0.318	0.115	0.095
N+P	0.014	0.416	0.140	0.101
N+P	0.013	0.486	0.157	0.115
N+P	0.007	0.171	0.062	0.045
N+P	0.016	0.542	0.179	0.132
N+P	0.033	0.334	0.131	0.117
N+P	0.026	0.287	0.108	0.083
N+P	0.015	0.637	0.200	0.162
N+P	0.028	0.662	0.215	0.177
N+P	0.010	0.599	0.190	0.139
Micro	0.014	0.046	0.023	0.022
Micro	0.010	0.119	0.039	0.033
Micro	0.035	0.165	0.075	0.068
Micro	0.017	0.106	0.044	0.038
Micro	0.024	0.143	0.060	0.054
Micro	0.078	0.244	0.136	0.128
Micro	0.082	0.183	0.118	0.112
Micro	0.042	0.178	0.079	0.072
Micro	0.045	0.131	0.057	0.051
Micro	0.018	0.238	0.087	0.074
Micro	0.066	0.191	0.106	0.099
Micro	0.122	0.248	0.174	0.170
Micro	0.076	0.138	0.074	0.069
Micro	0.013	0.091	0.036	0.031
Micro	0.008	0.091	0.035	0.031
Micro	0.010	0.101	0.035	0.029
Micro	0.007	0.104	0.035	0.028
Micro	0.010	0.079	0.030	0.025
Total	0.007	0.492	0.153	0.113
Total	0.013	0.880	0.275	0.200
Total	0.015	0.359	0.120	0.090
Total	0.008	0.609	0.186	0.140
Total	0.018	0.439	0.135	0.107
Total	0.066	0.632	0.228	0.200

Experiment #1

treatment	750nm	664nm	647nm	630nm
N, 100%	0.016	0.037	0.026	0.023
N, 100%	0.011	0.044	0.022	0.016
N, 100%	0.004	0.023	0.013	0.009
N, 100%	0.003	0.046	0.021	0.014
N, 100%	0.001	0.036	0.016	0.010
N, 100%	0.014	0.026	0.021	0.021
N, 70%	0.016	0.043	0.027	0.024
N, 70%	0.003	0.032	0.016	0.010
N, 70%	0.003	0.015	0.007	0.006
N, 70%	0.005	0.048	0.021	0.014
N, 70%	0.001	0.047	0.016	0.012
N, 70%	0.019	0.047	0.029	0.023
N, 37%	0.001	0.020	0.007	0.006
N, 37%	0.005	0.015	0.008	0.007
N, 37%	0.001	0.008	0.004	0.002
N, 37%	0.015	0.056	0.033	0.027
N, 37%	0.001	0.021	0.009	0.005
N, 37%	0.007	0.021	0.013	0.012
P, 100%	0.024	0.036	0.032	0.031
P, 100%	0.005	0.033	0.016	0.013
P, 100%	0.003	0.012	0.007	0.006
P, 100%	0.006	0.038	0.006	0.005
P, 100%	0.005	0.046	0.022	0.015
P, 100%	0.002	0.027	0.020	0.015
P, 70%	0.006	0.022	0.013	0.010
P, 70%	0.006	0.017	0.012	0.010
P, 70%	0.067	0.078	0.058	0.057
P, 70%	0.017	0.080	0.012	0.009
P, 70%	0.002	0.043	0.039	0.033
P, 70%	0.004	0.060	0.017	0.012
P, 37%	0.006	0.012	0.008	0.009
P, 37%	0.006	0.018	0.024	0.016
P, 37%	0.002	0.010	0.011	0.009
P, 37%	0.001	0.024	0.006	0.005
P, 37%	0.007	0.018	0.010	0.006
P, 37%	0.014	0.023	0.017	0.016
N+P, 100%	0.005	0.022	0.014	0.013
N+P, 100%	0.003	0.021	0.012	0.012
N+P, 100%	0.004	0.031	0.014	0.010
N+P, 100%	0.001	0.011	0.006	0.014
N+P, 100%	0.015	0.042	0.026	0.005
N+P, 100%	0.012	0.016	0.008	0.022
N+P, 70%	0.003	0.014	0.007	0.006
N+P, 70%	0.004	0.053	0.021	0.016
N+P, 70%	0.016	0.031	0.024	0.023

N+P, 70%	0.001	0.017	0.007	0.005
N+P, 70%	0.007	0.041	0.020	0.015
N+P, 70%	0.002	0.043	0.016	0.012
N+P, 37%	0.002	0.008	0.005	0.005
N+P, 37%	0.007	0.025	0.015	0.012
N+P, 37%	0.021	0.033	0.025	0.024
N+P, 37%	0.046	0.065	0.056	0.055
N+P, 37%	0.040	0.050	0.044	0.042
N+P, 37%	0.011	0.027	0.017	0.015
Micro, 100%	0.002	0.058	0.027	0.016
Micro, 100%	0.007	0.063	0.034	0.024
Micro, 100%	0.003	0.074	0.033	0.021
Micro, 100%	0.006	0.124	0.058	0.037
Micro, 100%	0.003	0.106	0.050	0.029
Micro, 100%	0.006	0.152	0.072	0.045
Micro, 70%	0.003	0.070	0.032	0.021
Micro, 70%	0.002	0.062	0.029	0.018
Micro, 70%	0.001	0.059	0.026	0.016
Micro, 70%	0.003	0.124	0.055	0.031
Micro, 70%	0.007	0.193	0.085	0.051
Micro, 70%	0.007	0.191	0.083	0.049
Micro, 37%	0.002	0.037	0.017	0.011
Micro, 37%	0.005	0.076	0.036	0.024
Micro, 37%	0.056	0.110	0.085	0.082
Micro, 37%	0.005	0.048	0.021	0.015
Micro, 37%	0.022	0.071	0.040	0.032
Micro, 37%	0.007	0.047	0.024	0.016
Total, 100%	0.001	0.017	0.009	0.006
Total, 100%	0.001	0.017	0.010	0.006
Total, 100%	0.001	0.021	0.011	0.006
Total, 100%	0.023	0.076	0.047	0.040
Total, 100%	0.007	0.057	0.027	0.020
Total, 100%	0.035	0.110	0.066	0.057
Total, 70%	0.007	0.024	0.016	0.015
Total, 70%	0.006	0.031	0.017	0.013
Total, 70%	0.010	0.031	0.020	0.016
Total, 70%	0.031	0.101	0.062	0.051
Total, 70%	0.007	0.067	0.031	0.022
Total, 70%	0.006	0.075	0.034	0.022
Total, 37%	0.002	0.020	0.010	0.006
Total, 37%	0.004	0.015	0.007	0.006
Total, 37%	0.003	0.021	0.011	0.007
Total, 37%	0.004	0.022	0.011	0.009
Total, 37%	0.079	0.124	0.103	0.099
Total, 37%	0.007	0.030	0.016	0.011
Control, 100%	0.003	0.007	0.006	0.005
Control, 100%	0.026	0.034	0.032	0.033

Control, 100%	0.004	0.007	0.006	0.005
Control, 100%	0.006	0.050	0.025	0.016
Control, 100%	0.027	0.031	0.023	0.021
Control, 100%	0.007	0.036	0.019	0.014
Control, 70%	0.007	0.012	0.007	0.008
Control, 70%	0.002	0.022	0.011	0.008
Control, 70%	0.007	0.017	0.012	0.011
Control, 70%	0.011	0.086	0.040	0.028
Control, 70%	0.006	0.033	0.017	0.011
Control, 70%	0.006	0.057	0.027	0.018
Control, 37%	0.003	0.021	0.011	0.007
Control, 37%	0.048	0.064	0.058	0.055
Control, 37%	0.006	0.012	0.007	0.007
Control, 37%	0.003	0.005	0.004	0.004
Control, 37%	0.009	0.028	0.017	0.015
Control, 37%	0.003	0.016	0.010	0.006

Experiment #2

treatment	750nm	664nm	647nm	630nm
N, 100%	0.004	0.005	0.006	0.007
N, 100%	0.002	0.002	0.001	0.002
N, 100%	0.003	0.003	0.002	0.002
N, 100%	0.003	0.003	0.003	0.003
N, 100%	0.003	0.003	0.003	0.002
N, 100%	0.003	0.003	0.003	0.003
N, 70%	0.002	0.002	0.000	0.001
N, 70%	0.002	0.002	0.000	0.001
N, 70%	0.002	0.002	0.002	0.002
N, 70%	0.005	0.018	0.010	0.007
N, 70%	0.007	0.010	0.009	0.007
N, 70%	0.004	0.005	0.005	0.003
N, 37%	0.004	0.004	0.004	0.003
N, 37%	0.000	0.000	0.000	0.001
N, 37%	0.000	0.000	0.000	0.000
N, 37%	0.004	0.004	0.003	0.002
N, 37%	0.007	0.007	0.007	0.007
N, 37%	0.009	0.010	0.010	0.008
P, 100%	0.003	0.004	0.003	0.002
P, 100%	0.008	0.009	0.009	0.008
P, 100%	0.006	0.006	0.006	0.006
P, 100%	0.007	0.007	0.007	0.007
P, 100%	0.008	0.009	0.010	0.008
P, 100%	0.006	0.007	0.008	0.007
P, 70%	0.004	0.004	0.004	0.003
P, 70%	0.005	0.005	0.005	0.004
P, 70%	0.006	0.007	0.008	0.007
P, 70%	0.029	0.036	0.034	0.033
P, 70%	0.007	0.009	0.008	0.007
P, 70%	0.018	0.025	0.023	0.022
P, 37%	0.003	0.003	0.003	0.002
P, 37%	0.008	0.008	0.008	0.008
P, 37%	0.002	0.003	0.004	0.003
P, 37%	0.004	0.004	0.004	0.003
P, 37%	0.022	0.023	0.023	0.023
P, 37%	0.005	0.005	0.005	0.004
N+P, 100%	0.006	0.008	0.008	0.007
N+P, 100%	0.017	0.023	0.020	0.019
N+P, 100%	0.006	0.010	0.008	0.007
N+P, 100%	0.005	0.012	0.008	0.006
N+P, 100%	0.005	0.010	0.010	0.012
N+P, 100%	0.007	0.012	0.010	0.008
N+P, 70%	0.005	0.015	0.009	0.006
N+P, 70%	0.006	0.015	0.010	0.010
N+P, 70%	0.006	0.010	0.009	0.007

N+P, 70%	0.004	0.016	0.010	0.006
N+P, 70%	0.005	0.019	0.010	0.007
N+P, 70%	0.004	0.020	0.011	0.005
N+P, 37%	0.004	0.010	0.014	0.013
N+P, 37%	0.004	0.005	0.004	0.003
N+P, 37%	0.000	0.000	0.000	0.001
N+P, 37%	0.004	0.005	0.004	0.003
N+P, 37%	0.004	0.004	0.004	0.003
N+P, 37%	0.005	0.005	0.005	0.005
Micro, 100%	0.031	0.039	0.039	0.037
Micro, 100%	0.002	0.003	0.004	0.003
Micro, 100%	0.016	0.017	0.018	0.018
Micro, 100%	0.008	0.008	0.008	0.007
Micro, 100%	0.022	0.023	0.023	0.023
Micro, 100%	0.009	0.010	0.010	0.010
Micro, 70%	0.021	0.027	0.026	0.025
Micro, 70%	0.004	0.007	0.009	0.005
Micro, 70%	0.014	0.019	0.018	0.017
Micro, 70%	0.005	0.005	0.005	0.004
Micro, 70%	0.003	0.009	0.005	0.003
Micro, 70%	0.009	0.010	0.010	0.009
Micro, 37%	0.005	0.005	0.005	0.004
Micro, 37%	0.007	0.009	0.008	0.007
Micro, 37%	0.003	0.004	0.003	0.003
Micro, 37%	0.005	0.005	0.005	0.005
Micro, 37%	0.027	0.028	0.028	0.028
Micro, 37%	0.005	0.006	0.007	0.006
Total, 100%	0.003	0.010	0.007	0.005
Total, 100%	0.014	0.020	0.019	0.018
Total, 100%	0.006	0.012	0.010	0.008
Total, 100%	0.009	0.022	0.017	0.013
Total, 100%	0.003	0.010	0.006	0.003
Total, 100%	0.004	0.010	0.009	0.006
Total, 70%	0.004	0.014	0.009	0.006
Total, 70%	0.003	0.012	0.008	0.005
Total, 70%	0.003	0.012	0.008	0.006
Total, 70%	0.005	0.064	0.029	0.017
Total, 70%	0.010	0.035	0.021	0.016
Total, 70%	0.006	0.007	0.008	0.007
Total, 37%	0.003	0.009	0.006	0.004
Total, 37%	0.003	0.005	0.004	0.002
Total, 37%	0.005	0.007	0.006	0.006
Total, 37%	0.013	0.042	0.039	0.037
Total, 37%	0.004	0.005	0.004	0.003
Total, 37%	0.008	0.009	0.009	0.008
Control, 100%	0.001	0.002	0.003	0.002
Control, 100%	0.003	0.003	0.003	0.002

Control, 100%	0.018	0.019	0.020	0.020
Control, 100%	0.003	0.004	0.005	0.004
Control, 100%	0.002	0.003	0.004	0.003
Control, 100%	0.006	0.013	0.011	0.008
Control, 70%	0.001	0.002	0.004	0.007
Control, 70%	0.008	0.009	0.009	0.007
Control, 70%	0.001	0.002	0.003	0.002
Control, 70%	0.001	0.002	0.002	0.002
Control, 70%	0.008	0.009	0.010	0.008
Control, 70%	0.007	0.008	0.007	0.007
Control, 37%	0.004	0.004	0.004	0.003
Control, 37%	0.000	0.000	0.000	0.002
Control, 37%	0.000	0.001	0.002	0.002
Control, 37%	0.018	0.019	0.020	0.020
Control, 37%	0.006	0.007	0.008	0.007
Control, 37%	0.004	0.005	0.006	0.006

Experiment #3

treatment	750nm	664nm	647nm	630nm
N, 100%	0.018	0.019	0.017	0.016
N, 100%	0.006	0.008	0.007	0.006
N, 100%	0.001	0.004	0.002	0.001
N, 100%	0.017	0.026	0.023	0.023
N, 100%	0.011	0.019	0.015	0.014
N, 100%	0.011	0.014	0.012	0.011
N, 70%	0.002	0.004	0.003	0.002
N, 70%	0.005	0.009	0.007	0.006
N, 70%	0.006	0.009	0.008	0.007
N, 70%	0.065	0.090	0.080	0.078
N, 70%	0.016	0.042	0.027	0.021
N, 70%	0.006	0.023	0.013	0.009
N, 37%	0.011	0.015	0.013	0.014
N, 37%	0.005	0.007	0.006	0.005
N, 37%	0.007	0.009	0.007	0.006
N, 37%	0.015	0.019	0.016	0.016
N, 37%	0.051	0.062	0.060	0.062
N, 37%	0.029	0.033	0.029	0.028
P, 100%	0.001	0.005	0.003	0.002
P, 100%	0.006	0.011	0.008	0.009
P, 100%	0.001	0.003	0.002	0.001
P, 100%	0.003	0.012	0.007	0.006
P, 100%	0.005	0.009	0.007	0.006
P, 100%	0.007	0.021	0.013	0.012
P, 70%	0.006	0.019	0.012	0.011
P, 70%	0.002	0.008	0.005	0.004
P, 70%	0.003	0.010	0.006	0.006
P, 70%	0.029	0.036	0.034	0.033
P, 70%	0.007	0.009	0.008	0.007
P, 70%	0.018	0.025	0.023	0.022
P, 37%	0.011	0.018	0.014	0.014
P, 37%	0.027	0.034	0.035	0.035
P, 37%	0.014	0.024	0.021	0.020
P, 37%	0.011	0.019	0.015	0.014
P, 37%	0.046	0.053	0.052	0.052
P, 37%	0.010	0.015	0.012	0.011
N+P, 100%	0.001	0.017	0.010	0.007
N+P, 100%	0.001	0.010	0.007	0.006
N+P, 100%	0.001	0.014	0.008	0.006
N+P, 100%	0.042	0.071	0.057	0.055
N+P, 100%	0.010	0.032	0.020	0.018
N+P, 100%	0.034	0.063	0.050	0.047
N+P, 70%	0.014	0.053	0.033	0.026
N+P, 70%	0.006	0.049	0.026	0.019
N+P, 70%	0.004	0.019	0.011	0.009

N+P, 70%	0.086	0.132	0.109	0.103
N+P, 70%	0.016	0.034	0.024	0.021
N+P, 70%	0.018	0.042	0.029	0.026
N+P, 37%	0.007	0.016	0.012	0.011
N+P, 37%	0.006	0.018	0.012	0.010
N+P, 37%	0.016	0.027	0.021	0.020
N+P, 37%	0.027	0.030	0.027	0.030
N+P, 37%	0.007	0.017	0.011	0.010
N+P, 37%	0.029	0.039	0.032	0.031
Micro, 100%	0.001	0.004	0.003	0.020
Micro, 100%	0.003	0.007	0.006	0.005
Micro, 100%	0.003	0.008	0.006	0.005
Micro, 100%	0.011	0.019	0.014	0.014
Micro, 100%	0.012	0.019	0.017	0.016
Micro, 100%	0.037	0.058	0.050	0.046
Micro, 70%	0.020	0.028	0.025	0.024
Micro, 70%	0.007	0.018	0.013	0.011
Micro, 70%	0.051	0.063	0.060	0.061
Micro, 70%	0.059	0.088	0.074	0.071
Micro, 70%	0.006	0.036	0.018	0.013
Micro, 70%	0.047	0.082	0.060	0.052
Micro, 37%	0.007	0.017	0.012	0.011
Micro, 37%	0.006	0.017	0.010	0.009
Micro, 37%	0.015	0.024	0.021	0.020
Micro, 37%	0.021	0.031	0.026	0.023
Micro, 37%	0.086	0.087	0.072	0.058
Micro, 37%	0.017	0.039	0.027	0.026
Total, 100%	0.002	0.019	0.011	0.007
Total, 100%	0.003	0.013	0.008	0.007
Total, 100%	0.004	0.009	0.008	0.006
Total, 100%	0.002	0.047	0.035	0.031
Total, 100%	0.045	0.073	0.055	0.050
Total, 100%	0.017	0.044	0.032	0.031
Total, 70%	0.004	0.017	0.010	0.007
Total, 70%	0.071	0.094	0.088	0.085
Total, 70%	0.008	0.029	0.018	0.016
Total, 70%	0.022	0.039	0.031	0.026
Total, 70%	0.036	0.096	0.063	0.058
Total, 70%	0.022	0.054	0.037	0.032
Total, 37%	0.007	0.017	0.012	0.011
Total, 37%	0.006	0.014	0.010	0.010
Total, 37%	0.010	0.023	0.016	0.015
Total, 37%	0.016	0.033	0.025	0.023
Total, 37%	0.032	0.040	0.037	0.035
Total, 37%	0.013	0.025	0.020	0.019
Control, 100%	0.006	0.009	0.008	0.009
Control, 100%	0.005	0.007	0.006	0.005

Control, 100%	0.007	0.009	0.008	0.008
Control, 100%	0.032	0.047	0.037	0.034
Control, 100%	0.022	0.034	0.028	0.026
Control, 100%	0.027	0.034	0.032	0.033
Control, 70%	0.006	0.007	0.006	0.005
Control, 70%	0.003	0.005	0.004	0.004
Control, 70%	0.025	0.028	0.027	0.028
Control, 70%	0.014	0.063	0.035	0.026
Control, 70%	0.011	0.032	0.020	0.016
Control, 70%	0.017	0.024	0.022	0.021
Control, 37%	0.005	0.006	0.004	0.004
Control, 37%	0.017	0.020	0.018	0.019
Control, 37%	0.011	0.015	0.013	0.014
Control, 37%	0.007	0.014	0.011	0.010
Control, 37%	0.013	0.019	0.016	0.016
Control, 37%	0.005	0.007	0.006	0.006

Experiment #4

treatment	750nm	664nm	647nm	630nm
N, 100%	0.001	0.002	-0.001	-0.003
N, 100%	0.012	0.013	0.012	0.011
N, 100%	0.008	0.009	0.007	0.006
N, 100%	0.014	0.016	0.022	0.028
N, 100%	0.039	0.044	0.043	0.042
N, 100%	0.072	0.077	0.073	0.071
N, 70%	0.008	0.012	0.010	0.010
N, 70%	0.013	0.014	0.010	0.010
N, 70%	0.020	0.024	0.023	0.025
N, 70%	0.032	0.043	0.039	0.042
N, 70%	0.073	0.093	0.088	0.087
N, 70%	0.059	0.118	0.091	0.081
N, 37%	0.020	0.024	0.024	0.024
N, 37%	0.021	0.025	0.024	0.024
N, 37%	0.062	0.104	0.106	0.102
N, 37%	0.022	0.028	0.027	0.027
N, 37%	0.126	0.162	0.181	0.184
N, 37%	0.025	0.042	0.041	0.036
P, 100%	0.141	0.152	0.157	0.161
P, 100%	0.001	0.001	-0.001	-0.002
P, 100%	0.011	0.011	0.010	0.009
P, 100%	0.030	0.050	0.042	0.040
P, 100%	0.024	0.033	0.028	0.028
P, 100%	0.036	0.045	0.044	0.044
P, 70%	0.046	0.062	0.057	0.058
P, 70%	0.056	0.066	0.065	0.065
P, 70%	0.004	0.018	0.010	0.009
P, 70%	0.065	0.086	0.077	0.073
P, 70%	0.064	0.123	0.098	0.090
P, 70%	0.054	0.106	0.090	0.065
P, 37%	0.024	0.029	0.028	0.028
P, 37%	0.073	0.078	0.078	0.079
P, 37%	0.013	0.016	0.015	0.014
P, 37%	0.034	0.042	0.039	0.040
P, 37%	0.010	0.012	0.011	0.012
P, 37%	0.020	0.030	0.020	0.030
N+P, 100%	0.020	0.024	0.023	0.022
N+P, 100%	0.003	0.005	0.004	0.004
N+P, 100%	0.006	0.019	0.013	0.011
N+P, 100%	0.005	0.008	0.005	0.005
N+P, 100%	0.114	0.121	0.113	0.112
N+P, 100%	0.003	0.008	0.005	0.004
N+P, 70%	0.037	0.056	0.051	0.050
N+P, 70%	0.013	0.041	0.027	0.022
N+P, 70%	0.013	0.027	0.020	0.018

N+P, 70%	0.004	0.026	0.013	0.009
N+P, 70%	0.020	0.063	0.037	0.029
N+P, 70%	0.010	0.050	0.027	0.018
N+P, 37%	0.010	0.016	0.013	0.013
N+P, 37%	0.004	0.013	0.007	0.006
N+P, 37%	0.004	0.012	0.007	0.007
N+P, 37%	0.005	0.008	0.005	0.007
N+P, 37%	0.009	0.014	0.010	0.010
N+P, 37%	0.010	0.014	0.014	0.014
Micro, 100%	0.105	0.118	0.120	0.119
Micro, 100%	0.013	0.020	0.019	0.018
Micro, 100%	0.019	0.024	0.023	0.026
Micro, 100%	0.005	0.011	0.009	0.008
Micro, 100%	0.014	0.021	0.018	0.018
Micro, 100%	0.059	0.079	0.073	0.073
Micro, 70%	0.025	0.037	0.029	0.025
Micro, 70%	0.025	0.049	0.043	0.039
Micro, 70%	0.008	0.016	0.012	0.010
Micro, 70%	0.039	0.050	0.042	0.039
Micro, 70%	0.027	0.055	0.040	0.035
Micro, 70%	0.032	0.064	0.049	0.044
Micro, 37%	0.020	0.026	0.025	0.026
Micro, 37%	0.007	0.016	0.011	0.011
Micro, 37%	0.004	0.010	0.005	0.005
Micro, 37%	0.103	0.121	0.117	0.120
Micro, 37%	0.178	0.195	0.185	0.174
Micro, 37%	0.004	0.006	0.004	0.005
Total, 100%	0.007	0.014	0.012	0.011
Total, 100%	0.004	0.008	0.006	0.005
Total, 100%	0.036	0.047	0.045	0.044
Total, 100%	0.019	0.024	0.021	0.022
Total, 100%	0.038	0.054	0.047	0.044
Total, 100%	0.006	0.058	0.026	0.020
Total, 70%	0.007	0.037	0.022	0.016
Total, 70%	0.023	0.066	0.043	0.036
Total, 70%	0.002	0.010	0.006	0.004
Total, 70%	0.063	0.085	0.078	0.077
Total, 70%	0.018	0.045	0.032	0.028
Total, 70%	0.017	0.074	0.043	0.034
Total, 37%	0.064	0.074	0.070	0.072
Total, 37%	0.030	0.035	0.029	0.028
Total, 37%	0.021	0.035	0.031	0.031
Total, 37%	0.010	0.015	0.012	0.012
Total, 37%	0.025	0.030	0.029	0.032
Total, 37%	0.005	0.010	0.008	0.008
Control, 100%	0.028	0.029	0.028	0.029
Control, 100%	0.008	0.010	0.010	0.010

Control, 100%	0.008	0.009	0.009	0.009
Control, 100%	0.034	0.043	0.040	0.040
Control, 100%	0.097	0.116	0.124	0.135
Control, 100%	0.025	0.035	0.034	0.037
Control, 70%	0.022	0.028	0.027	0.025
Control, 70%	0.047	0.067	0.067	0.064
Control, 70%	0.013	0.015	0.014	0.014
Control, 70%	0.093	0.153	0.150	0.151
Control, 70%	0.031	0.053	0.043	0.039
Control, 70%	0.064	0.111	0.088	0.081
Control, 37%	0.053	0.064	0.063	0.062
Control, 37%	0.011	0.015	0.014	0.014
Control, 37%	0.028	0.036	0.034	0.034
Control, 37%	0.024	0.028	0.025	0.024
Control, 37%	0.029	0.034	0.033	0.034
Control, 37%	0.078	0.092	0.089	0.090

Experiment #5

treatment	750nm	664nm	647nm	630nm
N, 10 cm	0.004	0.034	0.015	0.013
N, 10 cm	0.008	0.024	0.015	0.014
N, 10 cm	0.016	0.074	0.038	0.031
N, 10 cm	0.010	0.045	0.025	0.021
N, 10 cm	0.057	0.122	0.089	0.084
N, 10 cm	0.035	0.127	0.074	0.063
N, 25 cm	0.058	0.080	0.072	0.070
N, 25 cm	0.034	0.039	0.026	0.024
N, 25 cm	0.010	0.037	0.022	0.018
N, 25 cm	0.014	0.055	0.033	0.027
N, 25 cm	0.004	0.044	0.020	0.014
N, 25 cm	0.026	0.053	0.042	0.038
N, 40 cm	0.005	0.016	0.009	0.008
N, 40 cm	0.033	0.049	0.040	0.039
N, 40 cm	0.005	0.011	0.009	0.009
N, 40 cm	0.028	0.041	0.034	0.034
N, 40 cm	0.010	0.029	0.018	0.015
N, 40 cm	0.005	0.015	0.009	0.008
P, 10 cm	0.032	0.082	0.061	0.057
P, 10 cm	0.005	0.074	0.033	0.024
P, 10 cm	0.037	0.061	0.054	0.050
P, 10 cm	0.004	0.063	0.025	0.017
P, 10 cm	0.010	0.083	0.039	0.028
P, 10 cm	0.025	0.081	0.049	0.042
P, 25 cm	0.009	0.043	0.022	0.018
P, 25 cm	0.005	0.045	0.021	0.015
P, 25 cm	0.033	0.059	0.048	0.047
P, 25 cm	0.015	0.029	0.022	0.021
P, 25 cm	0.008	0.039	0.020	0.016
P, 25 cm	0.012	0.060	0.033	0.026
P, 40 cm	0.011	0.039	0.022	0.019
P, 40 cm	0.006	0.030	0.016	0.014
P, 40 cm	0.010	0.024	0.015	0.014
P, 40 cm	0.019	0.045	0.030	0.028
P, 40 cm	0.028	0.044	0.037	0.036
P, 40 cm	0.007	0.035	0.020	0.014
N+P, 10 cm	0.005	0.442	0.175	0.104
N+P, 10 cm	0.021	0.400	0.174	0.109
N+P, 10 cm	0.004	0.136	0.067	0.042
N+P, 10 cm	0.007	0.356	0.140	0.081
N+P, 10 cm	0.002	0.184	0.071	0.041
N+P, 10 cm	0.016	0.370	0.139	0.088
N+P, 25 cm	0.007	0.164	0.071	0.047
N+P, 25 cm	0.054	0.193	0.111	0.090
N+P, 25 cm	0.007	0.145	0.060	0.039

N+P, 25 cm	0.013	0.189	0.082	0.056
N+P, 25 cm	0.004	0.134	0.057	0.036
N+P, 25 cm	0.004	0.140	0.062	0.037
N+P, 40 cm	0.003	0.132	0.053	0.031
N+P, 40 cm	0.012	0.117	0.053	0.036
N+P, 40 cm	0.058	0.167	0.103	0.090
N+P, 40 cm	0.014	0.113	0.055	0.039
N+P, 40 cm	0.014	0.054	0.032	0.025
N+P, 40 cm	0.016	0.046	0.033	0.029
Micro, 10 cm	0.020	0.047	0.033	0.031
Micro, 10 cm	0.005	0.084	0.033	0.024
Micro, 10 cm	0.008	0.163	0.065	0.041
Micro, 10 cm	0.004	0.117	0.044	0.031
Micro, 10 cm	0.004	0.106	0.040	0.027
Micro, 10 cm	0.013	0.121	0.053	0.040
Micro, 25 cm	0.014	0.077	0.037	0.030
Micro, 25 cm	0.010	0.035	0.022	0.020
Micro, 25 cm	0.004	0.060	0.026	0.017
Micro, 25 cm	0.009	0.085	0.040	0.030
Micro, 25 cm	0.004	0.076	0.032	0.022
Micro, 25 cm	0.047	0.107	0.072	0.068
Micro, 40 cm	0.005	0.064	0.025	0.019
Micro, 40 cm	0.005	0.036	0.017	0.014
Micro, 40 cm	0.006	0.034	0.017	0.012
Micro, 40 cm	0.009	0.037	0.019	0.015
Micro, 40 cm	0.009	0.058	0.030	0.022
Micro, 40 cm	0.043	0.082	0.058	0.051
Total, 10 cm	0.004	0.124	0.057	0.037
Total, 10 cm	0.017	0.340	0.142	0.090
Total, 10 cm	0.004	0.264	0.107	0.062
Total, 10 cm	0.004	0.345	0.115	0.077
Total, 10 cm	0.004	0.336	0.125	0.079
Total, 10 cm	0.014	0.268	0.110	0.074
Total, 25 cm	0.028	0.100	0.061	0.051
Total, 25 cm	0.004	0.206	0.083	0.051
Total, 25 cm	0.004	0.210	0.082	0.050
Total, 25 cm	0.057	0.180	0.110	0.093
Total, 25 cm	0.032	0.184	0.089	0.061
Total, 25 cm	0.016	0.111	0.053	0.039
Total, 40 cm	0.024	0.068	0.045	0.041
Total, 40 cm	0.004	0.150	0.059	0.037
Total, 40 cm	0.003	0.107	0.042	0.027
Total, 40 cm	0.008	0.070	0.032	0.022
Total, 40 cm	0.021	0.086	0.048	0.041
Total, 40 cm	0.004	0.054	0.023	0.016
Control, 10 cm	0.029	0.089	0.048	0.041
Control, 10 cm	0.052	0.103	0.076	0.074

Control, 10 cm	0.008	0.072	0.029	0.022
Control, 10 cm	0.028	0.059	0.040	0.034
Control, 10 cm	0.014	0.118	0.053	0.039
Control, 10 cm	0.044	0.129	0.077	0.063
Control, 25 cm	0.047	0.057	0.053	0.056
Control, 25 cm	0.009	0.032	0.018	0.022
Control, 25 cm	0.011	0.035	0.021	0.018
Control, 25 cm	0.004	0.026	0.012	0.009
Control, 25 cm	0.020	0.048	0.032	0.030
Control, 25 cm	0.034	0.060	0.048	0.047
Control, 40 cm	0.048	0.058	0.057	0.057
Control, 40 cm	0.001	0.027	0.009	0.006
Control, 40 cm	0.004	0.019	0.009	0.007
Control, 40 cm	0.007	0.038	0.019	0.014
Control, 40 cm	0.017	0.037	0.025	0.024
Control, 40 cm	0.062	0.102	0.081	0.073

Appendix E

Statistical Summary

Pilot

Kruskal-Wallis One Way ANOVA on Ranks

Factor	df	H	P
nutrient	5	83.7	<0.0001

Experiments #1-5 Two-Way ANOVAs, Balanced Design

Experiment #1

Factor	df	F	P
light	2	11.66	<0.0001
nutrient	5	21.87	<0.0001
light x nutrient	10	1.22	0.2871

Experiment #2

Factor	df	F	P
light	2	6.82	<0.0001
nutrient	5	7.75	0.0018
light x nutrient	10	1.21	0.2969

Experiment #3

Factor	df	F	P
light	2	13.16	<0.0001
nutrient	5	7.95	<0.0001
light x nutrient	10	1.24	0.2778

Experiment #4

Factor	df	F	P
light	2	21.17	0.6994
nutrient	5	0.60	<0.0001
light x nutrient	10	1.08	0.3835

Experiment #5

Factor	df	F	P
light	2	49.71	<0.0001
nutrient	5	45.76	<0.0001
light x nutrient	10	6.43	<0.0001

VITA

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Master of Science

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