THE EFFECTS OF CHRONIC LIGHT REDUCTION ON *THALASSIA TESTUDINUM* AT STATIONS ACROSS THE GULF OF MEXICO

Final Report to the EPA Environmental Research Laboratory - Gulf Breeze

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I. INTRODUCTION

For several decades, the role and importance of seagrasses as habitat and as a trophic source, whether grazed directly, consumed as detritus, or acting as a means of support for epiphytic algae, has been increasingly well-documented in the coastal zones of the world. However, the environmental factors that influence the development and overall health of seagrass communities are much less well understood. While we know that acute, dramatic reductions in light levels have a negative effect on the growth and survival of seagrasses, there is limited information on the responses of these plants to lesser but chronic light reductions associated with phenomena such as persistent phytoplankton blooms and increased sediment loads.

There have been significant declines in seagrass coverage in many parts of the world related to reduced water quality and increased turbidity (Orth & Moore, 1983; Cambridge & McComb, 1984; Giesen et al., 1990; Larkum & West, 1990). The primary causes for increased turbidity are erosion of silt substrates, pollution, algal growth, ship and barge traffic and dredging activities (Peres & Picard, 1975; Cambridge & McComb, 1984; Cambridge et al., 1986; Onuf, 1994). Although seagrass growth and survival is largely related to light availability, there is a considerable amount of variability among species. Duarte (1991) reported an average minimum light requirement of 10.8% of surface irradiance (SI) for seagrasses from a worldwide survey of their maximum colonization depth. However, Dennison et al. (1993) reported that the estimated minimum light requirements for various seagrass species probably ranges from 4% to 25% SI. These variations are probably a result of the unique physiological and morphological adaptations among species and locations. Photoadaptive responses of seagrasses to reductions in irradiance have been reflected in some species by increases in chlorophyll (chl) content and decreases in biomass, growth rate, shoot density and chl a : b ratios (Backman & Barilotti, 1976; Wiginton & McMillan, 1979; Dennison & Alberte, 1982, 1985, 1986; Bay, 1984; Neverauskas, 1988; Tomasko & Dawes, 1989; Abal et al., 1994).

Thalassia testudinum is one of the most important seagrass species along the coasts of the Caribbean and the Gulf of Mexico and is the subject of this study. It is the climax species across the region, and typically the community dominant, usually by a large amount. *Thalassia* consists of horizontal rhizomes which branch at regular intervals, and erect short shoots (vertical rhizome) bearing foliage leaves and roots (Tomlinson & Vargo, 1966). This species constructs very dense rhizome systems and has differentiated vertical rhizome tissue (Duarte et al., 1994). Because of its relatively large leaves and basal leaf growth, it is much easier to measure growth and production than any of the other Gulf and Caribbean seagrasses (Zieman, 1974). In this study, we examined changes in leaf elongation, biomass, carbohydrate carbon content, blade width, chlorophyll content and chl *a* : *b* ratios in response to *in situ* light manipulations in *Thalassia*. We also investigated changes in biomass and carbohydrate carbon partitioning to different plant parts as a result of changes in underwater irradiance to determine the effect of light reduction on the partitioning of carbon in *Thalassia*. Continuous measurements of underwater quantum irradiance were made to document the amount of light received by plants in each shaded treatment. We also monitored changes in pore water ammonium and sulfide levels to assess sediment anoxia.

This research was undertaken as a multi-site study specifically addressing chronic light reduction and the responses of the seagrass community to this stress. There is a vital need for information in this area in light of the critical condition of the seagrass communities located throughout the Gulf of Mexico. The major field sites were located at Florida Bay at the southern tip of Florida, St. Joseph Bay in the northern Florida Panhandle, and Corpus Christi Bay on the western Texas coast (Fig. 1-1). The Florida Bay sites are subtropical and in recent decades were clear water sites where the seagrasses were rooted in biogenically derived carbonate sediments. St. Joseph's Bay is clear, but the seagrasses are in clastic sediments and the climate is warm temperate. The Corpus Christi Bay site is midway in latitude between the other sites, but is climatically temperate due to winter cold fronts. The sediments here are clastic and the water is historically the most turbid of the three sites.. More complete site descriptions are given in Chapters II-IV. Throughout the course of this project, each of the major field sites experienced one or more severe stresses, several of

environmental conditions, initially caused the direct loss of over 4,000 ha of seagrasses, largely *Thalassia*, totally denuded and an additional 23,000 ha severely affected (Robblee et al, 1991). While the initial dieoff has subsided, secondary algal blooms and turbidity plumes are blanketing hundreds of square kilometers, and causing general seagrass losses over wide areas. In Texas, protracted brown tides have for many years now periodically covered seagrass sites. St. Joseph Bay experienced stress in the form of heavy grazing pressure by sea urchins and a major rain event that dropped salinities to 10 ppt and the resulting influx from the watershed produced increased color in the water for a protracted time. These facts show the level of stress to which the communities in the coastal zone are being subjected around the entire periphery of the Gulf of Mexico.

This project was a response to the Coastal Submerged Aquatic Vegetation Initiative RFP, where the overall objective was to determine the response of seagrass communities to reduced levels of incoming light. Recent workshops and reports (Kenworthy and Haunert, 1991; Neckles, 1993) have agreed that a) historic standards of allowable light reduction are detrimental to seagrass communities, and b) chronic light reduction, due to suspended sediments, eutrophic algal growth, or a combination of the two, is the most important stress currently affecting submerged coastal vegetation. Historic estimates of compensation depth for aquatic plants has been the depth where 1 to 5% of the surface incident light remains. These values were based on studies of phytoplankton production (Ryther, 1956; Steemann-Nielsen, 1952). However recent studies show that seagrasses and aquatic macrophytes have much higher light compensation levels than phytoplankton because of the oxygen demand of roots, rhizomes, and lateral shoot bases (Chambers and Kalff, 1985). The report of a recent workshop on the light requirements of seagrasses estimated minimum light requirements of from 15 to 25% of the incident radiation (Abstracts and Summaries in

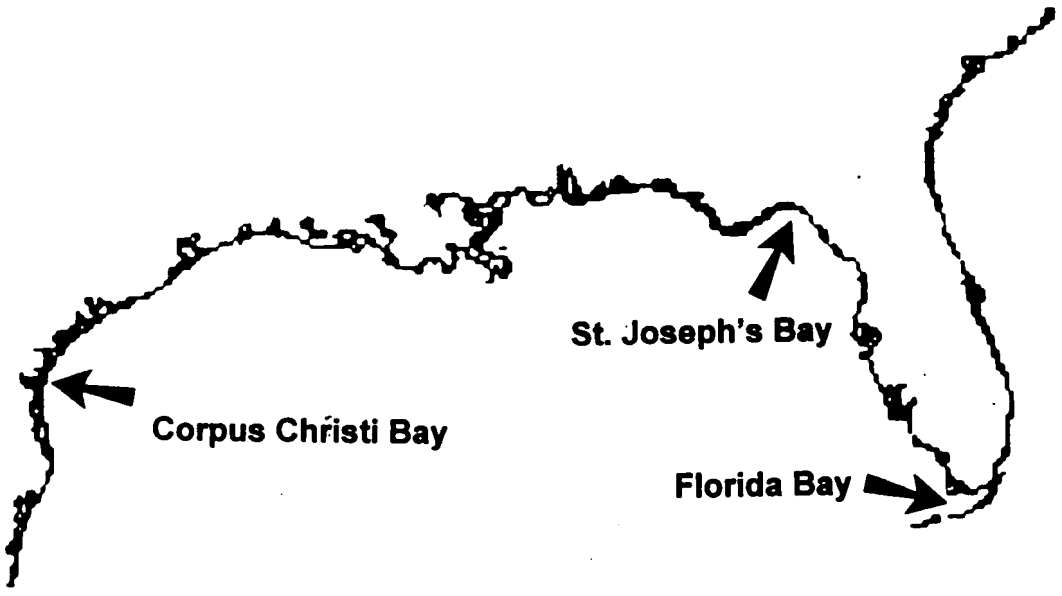


Fig. 1-1. General site map showing the locations of the main field sampling stations across the Gulf of Mexico. These are at Florida Bay, FL, at the southern tip of Florida, St. Joseph's Bay, FL, in the Florida panhandle, and Corpus Christi Bay, TX, on the south Texas coast.

report of a recent workshop on the light requirements of seagrasses estimated minimum light requirements of from 15 to 25% of the incident radiation (Abstracts and Summaries in Kenworthy and Haunert, 1991), while in a worldwide survey of maximum seagrass distribution, Duarte (1991) found the average maximum depth penetration to occur at 10.8% of surface radiation. These variations must, in part, be due to differing light attenuation components in the various waters and the differences in the architecture of the various seagrass species. *Thalassia testudinum* is one of the most robust and productive of all seagrasses, and has a very high investment in belowground tissue requiring considerable metabolic energy (Zieman, 1982; Fourqurean and Zieman, 1991).

In addition, in many areas the water quality standards are inadvertently drafted in such a way as to allow continued degradation. It might seem, for instance, that allowing certain environmental alterations that will reduce water clarity by only 10% might have little consequence. However, these standards rarely, if ever, reference the 10% reduction to historic water clarity, since it is often not known, and allow reduction from the present levels, which may already be significantly degraded from historic levels. Kenworthy and Haunert (1991) summarized this as follows:" Federal water color criteria and the Florida transparency standard utilize the compensation depth for photosynthetic activity as the parameter to delineate the minimum allowable light level. The standard and criteria stipulate that the depth of the compensation point not be reduced by more than 10% (substantially) compared to natural background. Because the history of significant human impacts to many coastal ecosystems is longer than the timeframe over which water quality monitoring has established natural background values, *the standards can only be used to maintain the status quo* (Italics added). A more comprehensive approach to water quality management must be adopted in order to increase light availability in environments which will support seagrass habitat."

Little research has addressed the chronic, subtle form of reduction of light to seagrasses. It is very easy to show negative effects on seagrasses by covering them with a blanket, and the effects occur rapidly. By contrast the effects of reducing light levels of healthy seagrass beds by 10 or 20 percent have not been well studied. This project coupled field and mesocosm research and examined physiological and ecological responses of *Thalassia* to reduced light availability.

CONCEPTUAL APPROACH This research approach utilized two related hypotheses of seagrass death following light stress: negative carbon balance and sulfide toxicity. Light quality and quantity affect seagrass growth, establishment, and survival by controlling carbon balance. The carbon balance of seagrasses is more complex than that of phytoplankton or macroalgae due to the increased structural complexity of the seagrasses, where carbon fixation in the leaves must supply the respiratory and growth requirements of the non-photosynthetic structures which make up as much as 90% of the biomass of *Thalassia* and can account for up to 60% of the respiration. Two methods of evaluating carbon balance have been utilized recently. One method measures P/I response of the whole plants oriented naturally in the light field (Fourqurean and Zieman, 1991). This method produces an ecologically relevant P/I curve. Another widely used technique (Dennison, 1987) measures the P/I response of leaf segments arranged perpendicularly to a light field and produces physiologically relevant P/I curves. While most of this project investigated whole-plant dynamics in the field cages, chapter VII utilized *Thalassia* leaf segments to estimate P/I relationships.

Sediment sulfide affects seagrasses in two important ways: 1) direct toxicity effects due to diffusion into roots and rhizomes, and 2) indirect effects due to chemical oxygen demand of the sediments on belowground tissue. The former effect is probably more acute, while chemical oxygen demand is a chronic burden on the oxygen status - and therefore, the carbon balance - of belowground tissue.

Many of the concepts implicit in the sulfide toxicity hypothesis are derived from shading studies, community metabolism measurements, and physiological studies by the Florida Department of Natural Resources (FDNR) of seagrass dieoff in Florida Bay: 1. Sulfide, a potent toxin produced as a major end-product of heterotrophic microbial metabolism in marine sediments is the primary agent of sediment chemical oxygen

demand in seagrass sediments. 2. Under non-limiting light levels, *Thalassia* is able to avoid sulfide toxicity by maintaining an oxidized rhizosphere. 3. However, when light becomes limiting or the internal oxygen supply of roots and rhizomes is interrupted by some other process, *Thalassia* may be affected by sulfide toxicity. 4. *Thalassia* is more prone to sulfide toxicity effects than are *Halodule* or *Syringodium* because *Thalassia* typically has a much higher root/shoot ratio than other species. In addition, experimentally elevated sediment sulfide concentrations in Florida Bay killed *Thalassia*, but not *Syringodium* or *Halodule*. The greatest sulfide toxicity effects are to be expected in carbonate sediment environments such as Florida Bay and least effects in sediments with high iron content.

Ethanol concentrations and alcohol dehydrogenase (ADH) activities of rhizome tissue will be used in field and mesocosm experiments as indices of sulfide-induced and shade-induced hypoxic stress within the belowground tissue of *Thalassia*. Many plant species produce ethanol by fermentation of acetaldehyde under anaerobic conditions, and ADH activity is often used to infer the intensity of hypoxic stress in plant tissues. ADH activity in Florida Bay *Thalassia* rhizomes is much higher than activities in *Thalassia* rhizomes from other Florida estuaries, perhaps as a result of higher sulfide-driven sediment COD in Florida Bay. Because fermentation produces only 2 moles of ATP for one mole of glucose (rather than 38 moles of ATP produced by aerobic respiration of one mole of glucose), we also infer from high ADH activity in *Thalassia* rhizomes that carbohydrate reserves may be rapidly depleted.

The principal objective of the study was to determine the responses of existing *Thalassia testudinum* meadow to chronic light reduction, and as a corollary to this determine the critical light level which determines the distribution of this seagrass species in the Gulf of Mexico. A series of secondary objectives were also addressed, including (1) a partial assessment of the physical and chemical requirements for optimal growth of *Thalassia* , (2) a preliminary evaluation of the utility of biomarkers, such as leaf chlorophyll and rhizome alcohol dehydrogenase (ADH) levels, as indicators of seagrass ecological health, (3) identification of factors responsible for light attenuation, and (4) examination of the potential synergistic effects of chronic light reduction and porewater sulfide levels on the survival and growth of *Thalassia testudinum*.

II METHODS AND MATERIALS - GENERAL

A common cage design and sampling protocol were developed for the program. Reduced light fields were achieved utilizing PVC-constructed cages covered with plastic mesh shade cloth. The cages were 1.5 m X 1.5 m X 0.5 m in dimension. Fine (0.64 cm) and coarse (2.54 cm) mesh sizes were used as cage tops to reduce PAR. The sides of the cages were covered with the coarse mesh in an attempt to keep out herbivorous grazers, specifically sea urchins, that would be attracted to structure. Control plots were constructed of the same areal dimensions with coarse mesh sides but without tops. The sediment at the perimeters of all nine plots (including the controls) were cut with a large saw to a depth of 40-50 cm at the initiation of the project to ensure physiological independence of the seagrasses within the plots (Harnett and Bazzaz, 1983; Tomasko and Dawes, 1989; Czerny and Dunton, 1995).

Initially we tested 20 different sizes and textures of mesh. While heavy nylon and polyethylene meshes such as Vexar have existed for some time, as this project began these materials were being made in the traditional black, and a new, translucent polymer. We had hoped the clear polymer would offer 10-15% light reduction, but the reduction was only 1-3%, useful for caging studies, but not for light reduction. The black Vexar worked fine, but instead of a gradient of light reduction, it grouped into two groupings despite a wide variety of mesh sizes and shapes. The reduction levels centered around 30% and 50% reduction, still quite useful for our purposes. For the high light treatment we selected 3/4" (1.91 cm) diamond Vexar mesh, with 70% transmission, and 1/4"(0.64 cm) diamond mesh with 50% transmission. All tests were done with Li-Cor spherical quantum sensors and LI-1000 recorders. Originally, for the best light control, the cages were installed at several sites with the meshes described above. We rapidly found however, that the 1/4" mesh size used as side panels reduce water flow too much, and retrofitted those cages with 3/4" mesh panels, which had

little effect on the flow.

The project was initiated in the spring of 1993. While there were no severe epiphyte problems at that time, by the middle of the summer of 1993, the single biggest problem that faced all of the sites was the cleaning of the cages. While this was not a serious problem in the spring months, it has become an immensely time-consuming task in the summer, the Texas site having to clean cages once a week, and in Florida the time period was at least every two weeks. Workers at the south Florida sites had the added problem that a large proportion of the fouling organisms were hydroids and the divers ended up working in a soup of shredded nematocysts.

As the cages became fouled, the resulting light to the plants declined until the next cleaning. This resulted in a much more severe light reduction, especially in the fine mesh cages than was originally intended and the plants in these cages declined. By the fall of 1993 the plants in the fine mesh cages were either greatly reduced (Florida Bay) or completely gone (Texas) , and a joint decision was made to remove the cages, but to maintain and monitor the plots for signs of recovery. Thus for the last year of the project we sampled the control areas, the coarse cages, and the abandoned fine mesh areas, the last to determine if any short-term recovery occurred.

Photon Flux Measurement Photosynthetically active radiation (PAR, 400-700 nm) was collected continuously using a LI-193SA spherical quantum sensor at canopy level, which provided input to a LI-1000 datalogger (LI-COR Inc.) enclosed in underwater housing. An underwater sensor was placed within one replicate of each of the three treatments and cleaned regularly to minimize fouling. Photon flux was measured at 1 min intervals and integrated hourly. At the Texas site, coincident measurements of incident surface PAR were made at The University of Texas Marine Science Institute (UTMSI) in Port Aransas, approximately 8 km from the study site, using a LI-190SA cosine corrected quantum sensor and LI-1000 datalogger. At the St. Joseph's Bay site, initial measurements were made both at the surface (ambient surface irradiance) and immediately above the seagrass bed canopy during sampling and cleaning periods. Measurements were also made within the treatment enclosures; these latter measurements were used in all light reduction calculations. Later this site used continuous recording similar to the other two sites

Biological Parameters

Plant response. Clipped shoots from the three 100 cm^2 areas within the enclosures and the three 47 cm^2 area cores from within each of these areas were used to provide information on leaf morphology, epiphyte loads, and seagrass above- and below-ground biomass. The harvested marked shoots of *Thalassia testudinum* were processed according to Zieman (1974); however, epiphytes were removed from the seagrass blades by gently scraping them from the leaf surface with a razor blade. This information was used to calculate the following plant response parameters: standing crop, areal production, turnover rate, leaf area index (LAI), and above- to below-ground biomass ratios.

At each site, twelve *Thalassia* short shoots within each enclosure (chosen arbitrarily) were perforated at the sediment-water interface with a 18 gauge syringe needle. The marked shoots were identified with surveyor's flags and bird bands. The marked leaves were allowed to grow for approximately two weeks, after which all marked short shoots were harvested at the sediment-water interface. All leaf material was gently scraped with a razor blade to remove epiphytic growth and then washed in fresh water. Leaf morphology was measured to the nearest millimeter. Unperforated leaves and portions of the leaves below the perforation, considered to be new growth, were separated from the rest of the leaf material. All leaf material was oven-dried at 85°C. Leaf turnover rate ($g \cdot g^{-1} \cdot day^{-1}$) was determined as the ratio of the dry weight of new growth to the total dry weight of attached leaves (above-ground standing crop) divided over the time of the growth period measured. At the time of leaf productivity harvesting, short shoot density was determined by counting the number of short shoots within 4 arbitrarily placed 10 cm X 10 cm quadrats within each enclosure at each site. Areal leaf

production rates were obtained by multiplying the leaf production rate per shoot by the shoot density

Biomass. For biomass, three replicate samples from each cage were collected with a 9 cm diameter coring device. *Thalassia* biomass was separated into tissue types according to the methods of Fourqurean and Zieman (1991). Samples were thoroughly cleaned of epiphytes and sediments, separated into leaf (blade and sheath), short stem (including vertical rhizome), rhizome and root and dried at 60°C to a constant weight. Shoot density was estimated by counting the number of shoots inside a randomly thrown quadrat (0.05 m^{-2}). *Halodule* biomass was separated into leaves and below ground components.

Chlorophyll. For determination of blade chlorophyll content, six replicate samples from each cage were collected and then cleaned of epiphytes in the laboratory. Pre-weighed leaf tissues were extracted for 4-5 days in glass screw cap tubes with 5 ml N,N-dimethyl formamide (DMF) following Dunton & Tomasko (1994). Absorbance of the extracts was measured at 750, 664 and 647 nm on a Shimadzu UV 160U spectrophotometer. Chl a and b contents were determined using the equations of Porra et al. (1989).

Epiphytic organisms. Ten blades were clipped from within each enclosure on a quarterly basis; these samples were preserved with 4% formalin; the presence of calcareous red algae at the study site dictated this as freezing tends to dislodge this material. The 10 blades collected from within each enclosure and preserved with 4% formalin were examined using a randomized grid system to determine the macroscopic epibionts present at each intersecting point. Epiphytes were essentially identified as functional groups; categories of macroscopic epibionts were as follows: green algae, brown algae, non-calcareous red algae, colonial ascidians, spirorbids, serpulids, and a generic category for encrusting calcareous epibionts, which included calcareous red algae and bryozoans.

Chemical Analyses On each sampling date four replicate sediment samples were collected to 10 cm depth from each shading treatment cage with a 60 ml syringe. Sediment pore water was obtained by centrifugation (5,000 xg for 15 min) and then diluted (1 : 5) with ammonium free seawater. Concentrations of NH_4^+ were determined using standard colorimetric techniques following the alternative method of Parsons et al. (1984).

Sediment pore water samples to determine sulfide concentration were collected with a pore water sampler under anaerobic conditions (Zimmermann et al., 1978) at the end of the experiment (August 1994). Samplers filled with nitrogen gas were inserted in the sediment and pore water surrounding the porous polyethylene frit was collected by the vacuum created with a 50 ml syringe. Dissolved sulfide content of pore water was determined colorimetrically according to Cline (1969). A 5-ml pore water sample was transferred to a test tube, to which 0.4 ml of the mixed diamine reagent was added under a nitrogen atmosphere. Color development was allowed to proceed in the dark for 30 min, after which the absorbance was determined spectrophotometrically at 670 nm. Dilutions were made after color development with distilled water. The concentrations of sulfide in the samples were calculated by standardization with known sulfide concentrations.

Dried plant materials from biomass samples were used to determine carbohydrate carbon content in different plant parts. Soluble carbohydrates from leaf, short stem, rhizome and root were determined using the MBTH (3-methyl-2-benzothiazolinone hydrazone hydrochloride) analysis (Parsons et al., 1984, Pakulski & Benner, 1992). Ground plant samples of 10 mg were hydrolyzed with 10 ml of 0.1 N HCl for 24 h at 100°C in a water bath to determine soluble carbohydrates. For determination of total carbohydrates, a hydrolysis using 12 M H_2SO_4 was conducted. The hydrolyzed samples were neutralized with 2 ml of 0.5 N NaOH, and 0.1 ml of the sample was diluted with 10 ml of persulfate distilled water in a serum vial. This sample was reduced with 0.25 ml of 10% KBH_4 for at least 4 hours in the dark, and acidified with 1 ml of 2N HCl to allow hydrogen gas to evolve. Triplicate 1 ml aliquots of hydrolysate from each sample serum vial were transferred to acid-washed and combusted (500°C, 4 hours) screw cap test tubes. Two additional 1 ml aliquots of hydrolysate were transferred to serve as blanks. Periodic acid solution (0.1 ml) was added to each of the three sample tubes and incubated for 10 min in the dark at room temperature. Sodium arsenite solution (0.1 ml) was added to each sample tube in order to stop the oxidation reaction. For analytical blanks, 0.2 ml of the sodium arsenite

and periodic acid mixture was pipetted into each of the two additional 1 ml of hydrolysate serving as blanks. The triplicate samples and duplicate blanks were acidified with 0.2 ml of 2 N HCl. Freshly prepared 0.2 ml of MBTH solution was added to both samples and blanks, after which the tightly-capped tubes were incubated for 3 min in a boiling water bath. The tubes were cooled to room temperature with tap water. Once cooled, 0.2 ml of ferric chloride solution was added to the tubes, followed by a 30 min incubation at room temperature in the dark for color development. After color development 1 ml of acetone was added to each tube and absorbances were measured immediately at 635 nm with a spectrophotometer. Mean corrected absorbances calculated by subtracting analytical blanks were compared with a glucose standard and converted to equivalent carbon values.

III FLORIDA BAY, FLORIDA , SITE

J.C. Zieman, T. Frankovich, and J.W. Fourqurean

MATERIALS AND METHODS

Study Sites The seagrass shading experiment was conducted at two sites within Florida Bay during the period from April 1993 to September 1994. Florida Bay is located at the southern tip of Florida between the Florida mainland and the Florida Keys (Fig. 3-1). Both study sites are approximately 1.5 m (MLW) in depth and are characterized by nutrient-limited seagrass meadows dominated by *Thalassia testudinum* with a sparse understory of *Halodule wrightii* (Zieman and Fourqurean, 1989; Fourqurean et al., 1992). Both sites have been affected by the recent and continuing *Thalassia* dieoff (Robblee et al., 1991) and associated algal blooms (Phlips and Badylak, 1996). Historically, the waters of Florida Bay were very clear (mean light extinction coefficient = 0.5 m^{-1}, Fourqurean and Zieman, 1991), but recent and continuing phytoplankton blooms have greatly reduced light penetration (Phlips et al., 1995). The Sunset Cove (SUN) site is located in eastern Florida Bay approximately 100 meters from the shoreline of Key Largo. SUN is not openly connected with either the Gulf of Mexico or the Atlantic Ocean, as such tidal influence is very limited. Sediment depths averaged 60 cm and the *Thalassia* was moderately dense (mean shoot density = 580 shoots $\cdot m^{-2}$; mean standing crop = 90 g m^{-2}). In contrast, the Rabbit Key Basin (RKB) site, in western Florida Bay, is affected by tidal influences from both the Gulf of Mexico and the Atlantic Ocean. The sediments are much deeper (130 cm) and the *Thalassia* was more dense (mean shoot density = 780 shoots $\cdot m^{-2}$), but individual shoots were smaller (mean standing crop = 82 g m^{-2})

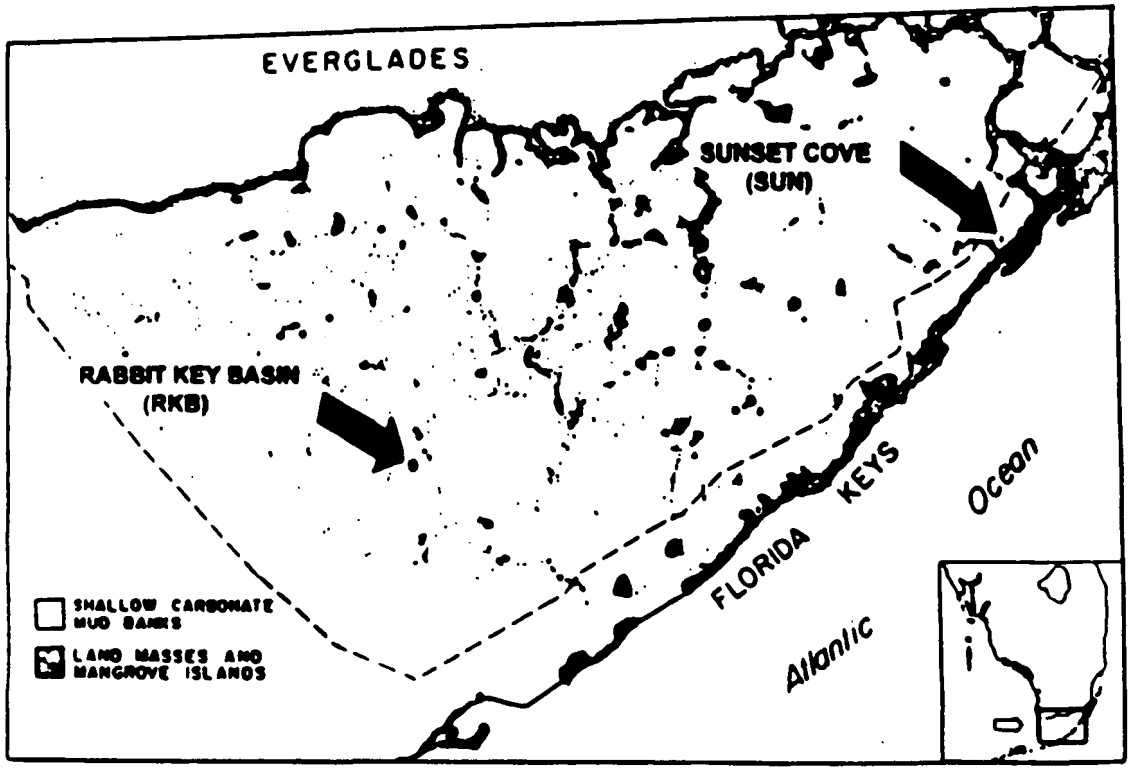


Fig. 3-1. Location map showing the two south Florida sites at Rabbit Key Basin (RKB) and Sunset Cove (SUN) in Florida Bay.

Experimental Design The seagrasses at both sites were exposed to three different light treatments (ambient, 30% and 60% of ambient in situ light) in order to monitor physical and biological changes resulting from a reduction in the intensity of PAR reaching the seagrasses. The three treatments were conducted in triplicate at each site. The shading cages were cleaned every two weeks, but bio-fouling reduced PAR to as little as 8% (fine) and 16% (coarse) of the in situ ambient light. After six months of shading treatment, in October 1993, all experimental plots at the Sunset Cove site were dismantled due to the death of all seagrass short shoots in the shaded cages (both fine and coarse). One month later, the shading screen tops were removed from the three fine screen cages at the Rabbit Key Basin site due to nearly complete shoot mortality.
Underwater measurements of photosynthetically active radiation (PAR, 400-700 nm) were recorded continuously in one plot of each treatment at each site. Three LI-193SA spherical (4π) quantum sensors provided input to a LI-1000 datalogger (LICOR, Inc., Lincoln, Nebraska USA) at each site.

Leaf Mark Productivity and Short Shoot Density *Thalassia testudinum* leaf productivity was measured during April, July, and September of 1993 at both sites and in April, July, and September of 1994 at just the Rabbit Key Basin site. The leaf marking method (Zieman, 1974, 1975; Frankovich and Zieman, 1994) was used to determine leaf productivity, leaf biomass, and leaf morphology.

Biomass Seagrass biomass (above-ground and below-ground) was measured during August and October of 1993 at both sites and during March, June, and September of 1994 at the remaining Rabbit Key Basin site. Biomass was measured using a PVC corer (diameter = 28 cm).

RESULTS

Physical Parameters

Photosynthetically Active Radiation. The way in which light data is recorded, processed, and presented can affect interpretation and comparison with other variables. In figure 3-2 PAR is plotted in the three treatments as monthly averages and maxima. The maxima are the highest value recorded for that month, while the averages are the mean of all daily averaged data for the month. At the controls, the means are about 40-50% of the maxima, while at the coarse treatment the means ran 20 to 35% of the maxima.

The PAR data is depicted differently in figure 3-3. Here the data for both SUN and RKB are plotted in average *Einsteins* or mol photon$\cdot m^{-2} \cdot d^{-1}$. This represents the daily and monthly integrated photon flux to the plants. What is most meaningful here, and is an important point is that the integrated flux values are attenuated to a greater extent than the average or maximum values by the epiphytic buildup on the cages, and probably by other forms of light attenuation, such as turbidity plumes and algal blooms, as well.

Temperature Temperatures throughout the project period were typical of Florida Bay, ranging from the upper 30's in the late summer to around 20°C in the winter. In the more open water of the basins, major upward excursions from these means are not as common as sudden drops below the means with the passing of winter cold fronts.

Salinity Over the period of this project, salinities at the two stations were moderate for Florida Bay. SUN ranged from 27.5 to 39 psu while RKB was slightly higher on the whole but more constant. SUN is a relatively enclosed cove with relatively poor circulation compared with RKB, and this is reflected by the rise in salinity in August and September 1993 in response to the elevated temperatures from July to September of the same year.

Of the temperature and salinity conditions monitored, the salinities should have been less stressful to the plants than the high temperatures encountered in the summer of 1993.

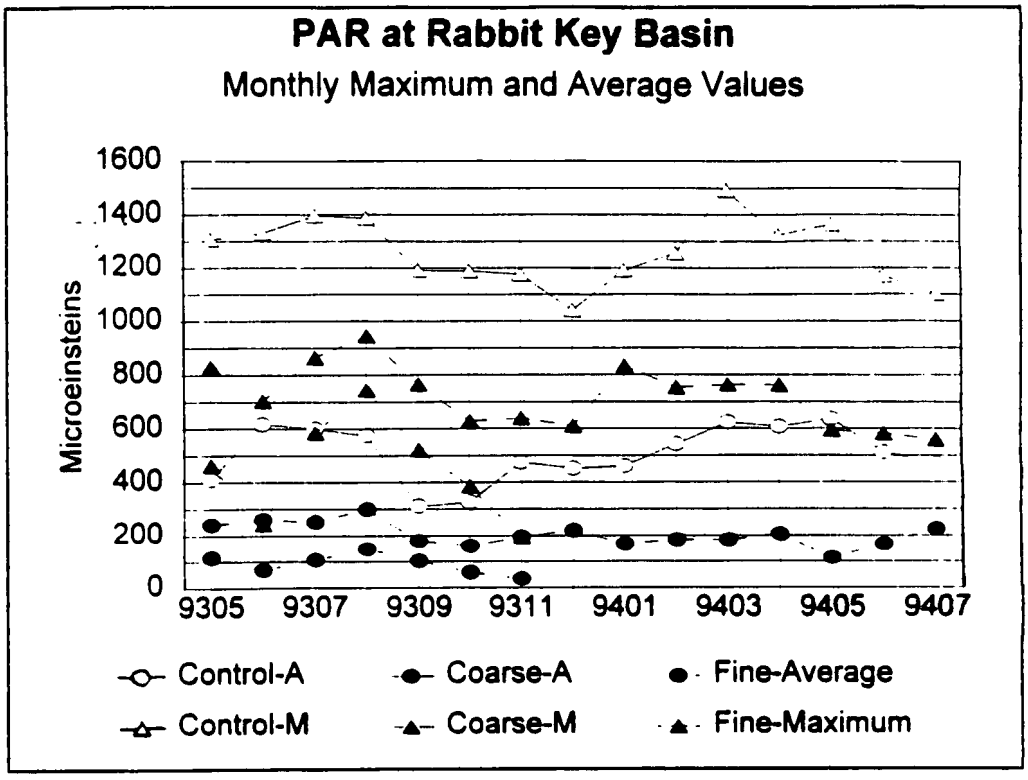


Fig. 3-2. Photosynthetically Active Radiation (PAR) for the Rabbit Key Basin (RKB) site. The circles represent the average daily intensity for the month depicted, and the triangles represent the maximum intensity recorded for that month.

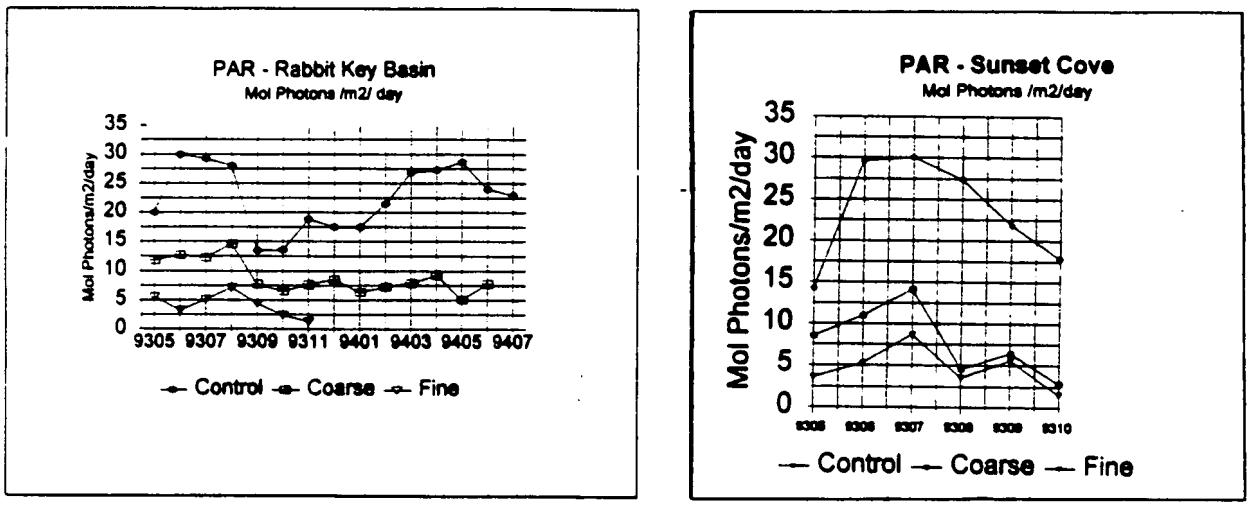


Fig. 3-3. PAR values for both Rabbit Key Basin and Sunset Cove for the period of the experiments. These values are monthly averages of the daily integrated PAR. For each month, they represent the total flux of photons received per day.

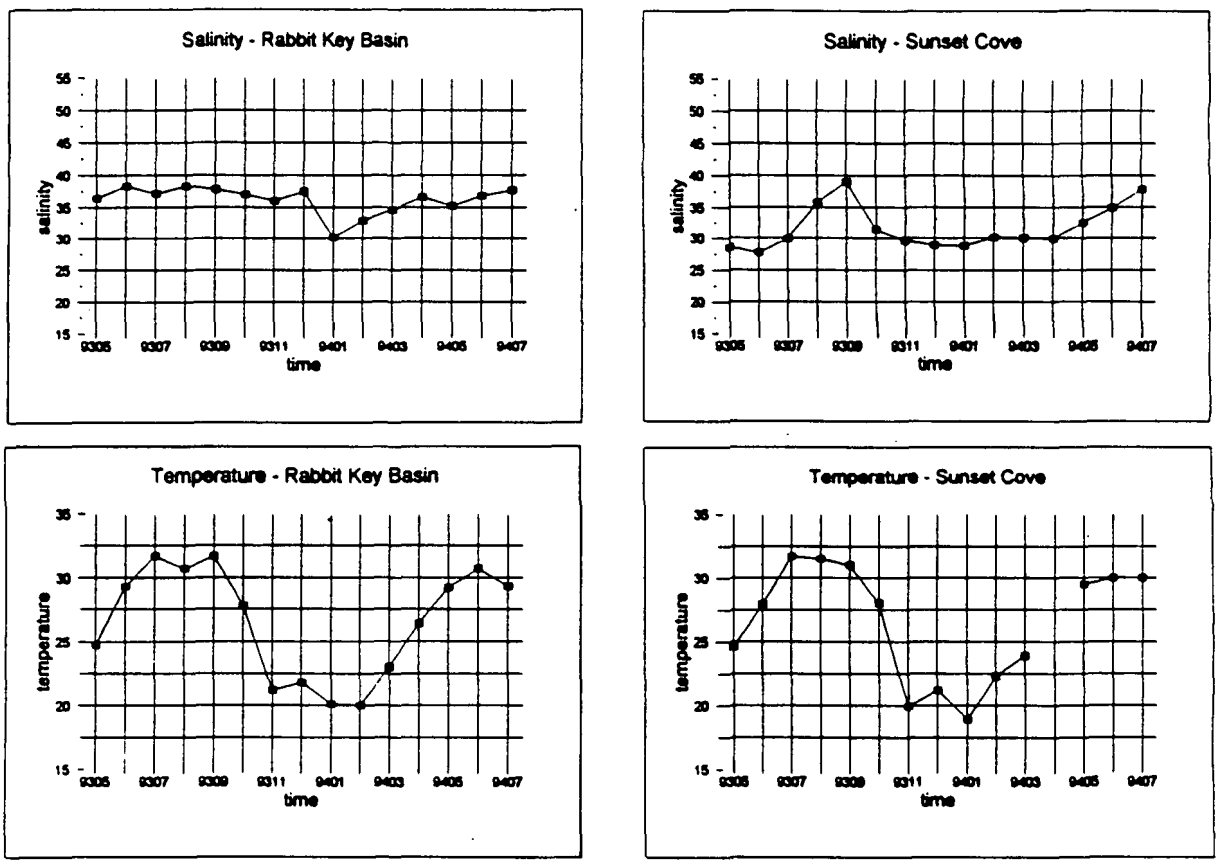


Fig. 3-4. Monthly averaged temperature and salinity for the stations in Rabbit Key Basin and Sunset Cove in Florida Bay.

Biotic Parameters

Leaf length showed a general increase at the SUN control stations and an overall increase at the RKB controls (Fig. 3-5 & 3-6). Initially there was little difference between the treatments, but progressively the shaded treatments declined relative to the control. At SUN the length of the coarse treatments was reduced to about 60% of the length of the control while the fine treatment showed an increase in September after declining strongly in the summer. RKB showed a seasonal variation, shorter in the cooler periods and longer in the warmer samplings. Leaf length in the treatment pens was similar to that of the control throughout the first year. By July of the second year, the length of leaves in the coarse treatment declined to near half the length in the control pens, while leaf lengths began to increase in the former fine treatment pens.

Leaf Width was initially the same at both sites (Fig. 3-5 & 3-6). At SUN, leaf widths of the treatments progressively declined, and by September 93 the control showed a decline also. In RKB, there was an initial decline by both treatments. The coarse mesh treatment continued to decline relative to the control, while the fine mesh treatment showed an increase in September 1993 and continued to remain the same as the control when the cages were removed.

Leaf Area Index incorporates input from leaf length, width, and density (Fig. 3-5 & 3-6). At SUN, the original LAI at initiation varied with the highest values at this time being in the coarse treatment. With time the LAI in the control plots increased, due largely to an increase in leaf length, while the treatments progressively declined, mainly due to a decrease in short shoot density. At RKB, the LAI in the control plots followed a seasonal trend, While there was a rapid and steady decrease in the LAI of the treatments relative to the control plots. When the fine mesh screens were removed, the LAI stabilized while it continued to decline in the coarse treatments. This decrease in the coarse mesh treatments was due to progressive declines in leaf length and short shoot density.

Short Shoot Density (Fig. 3-7 & 3-8) was actually higher at the treatment pens relative to the control pens in SUN at the initial sampling. The density declined linearly the coarse treatment. At the fine treatment pens the density was unchanged between April and July 1993 but dropped greatly by September 1993. At RKB all treatments were of similar densities initially. At the control pens the density did not show a seasonal pattern but increased in September 1993 and April 1994, but then decreased by September 1994 to a density similar to the initial density. (This seems to be inversely correlated with the PAR at RKB.) At the coarse treatment, the density also rose in the middle two sampling periods relative to its initial value, but declined relative to the control. By one year, the densities in the course treatments were below their initial levels and significantly below the density of the control pens. After 6 months treatment, the short shoot densities in the fine treatments decreased relatively to the control and coarse treatment. Despite removal of the fine mesh pens, this parameter continued to decline throughout the remainder of the experiment. This may indicate that short shoot density is a good indicator of chronic stress, as many other parameters showed a relatively rapid recovery at RKB following the removal of the fine treatment cages.

Leaves per Short Shoot In all cases, at the control stations, the lowest number of leaves per short shoot occurred in the September sampling (Fig. 3-7 & 3-8). At SUN there was steady decline from April to September. Both treatments decreased relative to the control and the fine mesh treatment decreased the most. At RKB the treatments declined relative to the control in 1993. In 1994 the number of leaves in the coarse treatment remained below the level of the control while the fine mesh treatment increased to greater than the control once the fine mesh was removed.

Leaf Standing Crop (Fig. 3-7 & 3-8) At SUN, while the standing crop in the coarse treatment was the highest in the initial sampling, by July 1993, both light-reduction treatments were below the control. By September 1993 the coarse treatment was only 50% of the control and the fine treatment was less than 25%. At RKB both

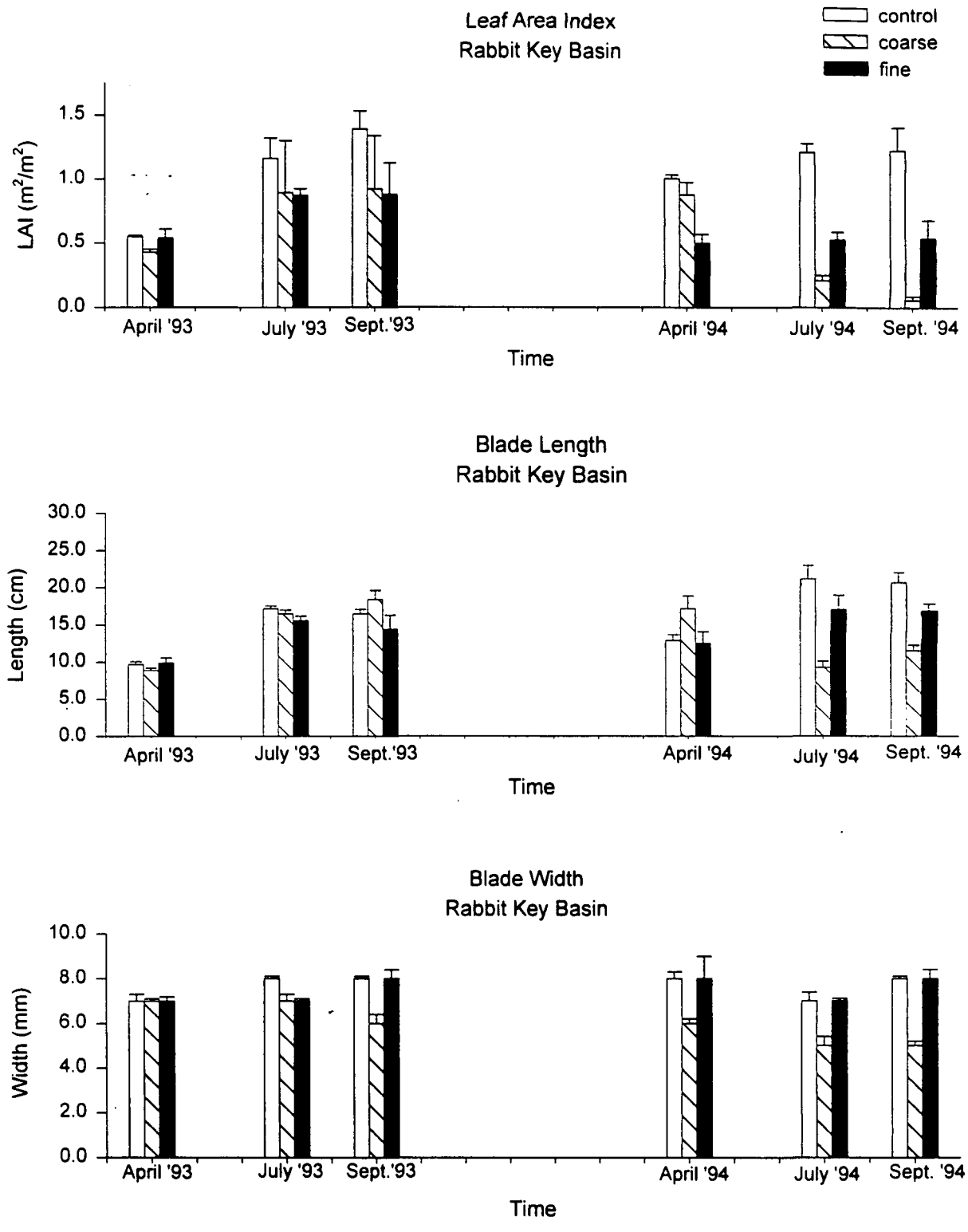


Fig. 3-5. Leaf length (cm), leaf width (mm), and leaf area index (LAI, m^2 /m^2) for the stations at Rabbit Key Basin.

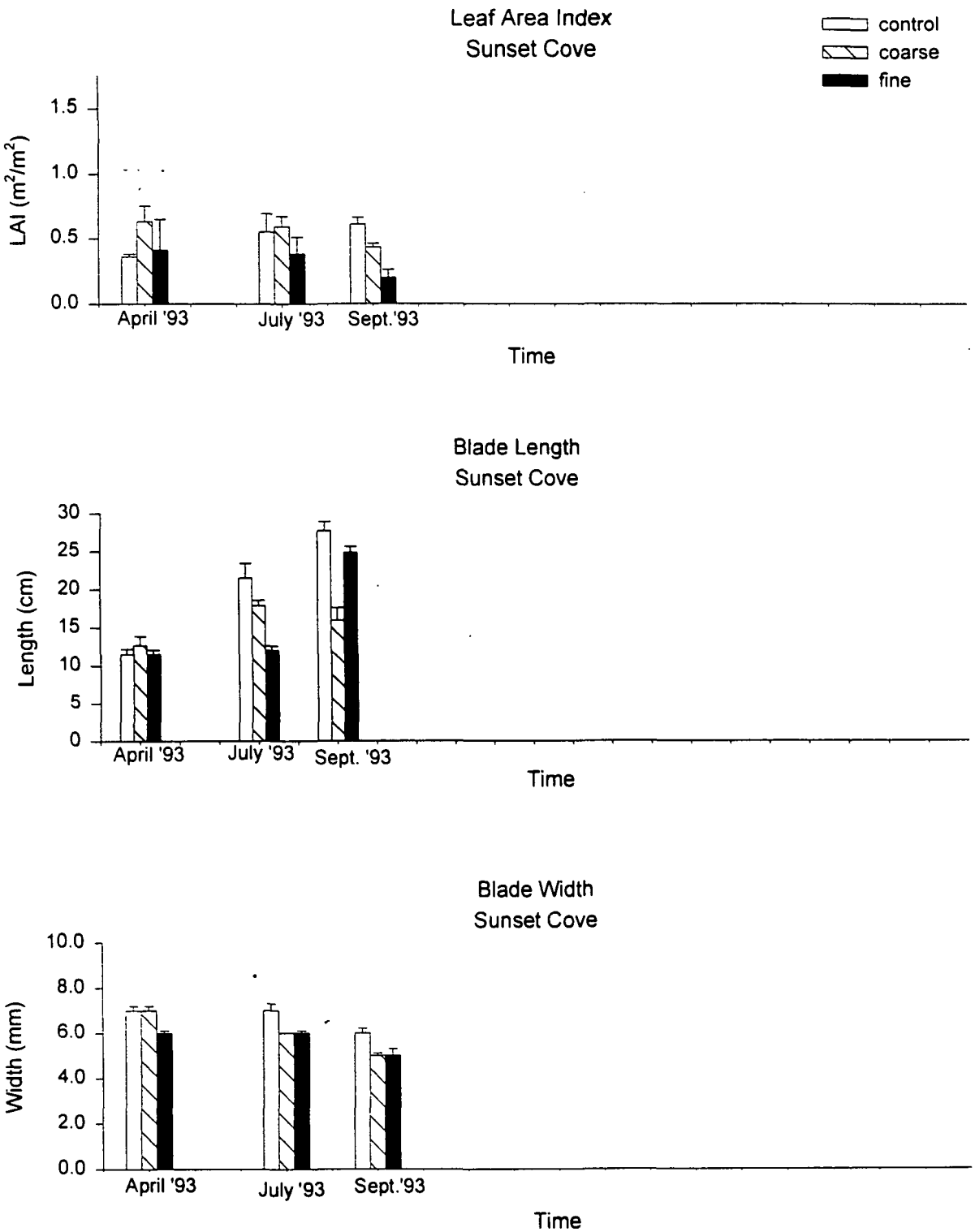


Fig. 3-6. Leaf length (cm), leaf width (mm), and leaf area index (LAI, m^2 /m^2) for the stations at Sunset Cove.

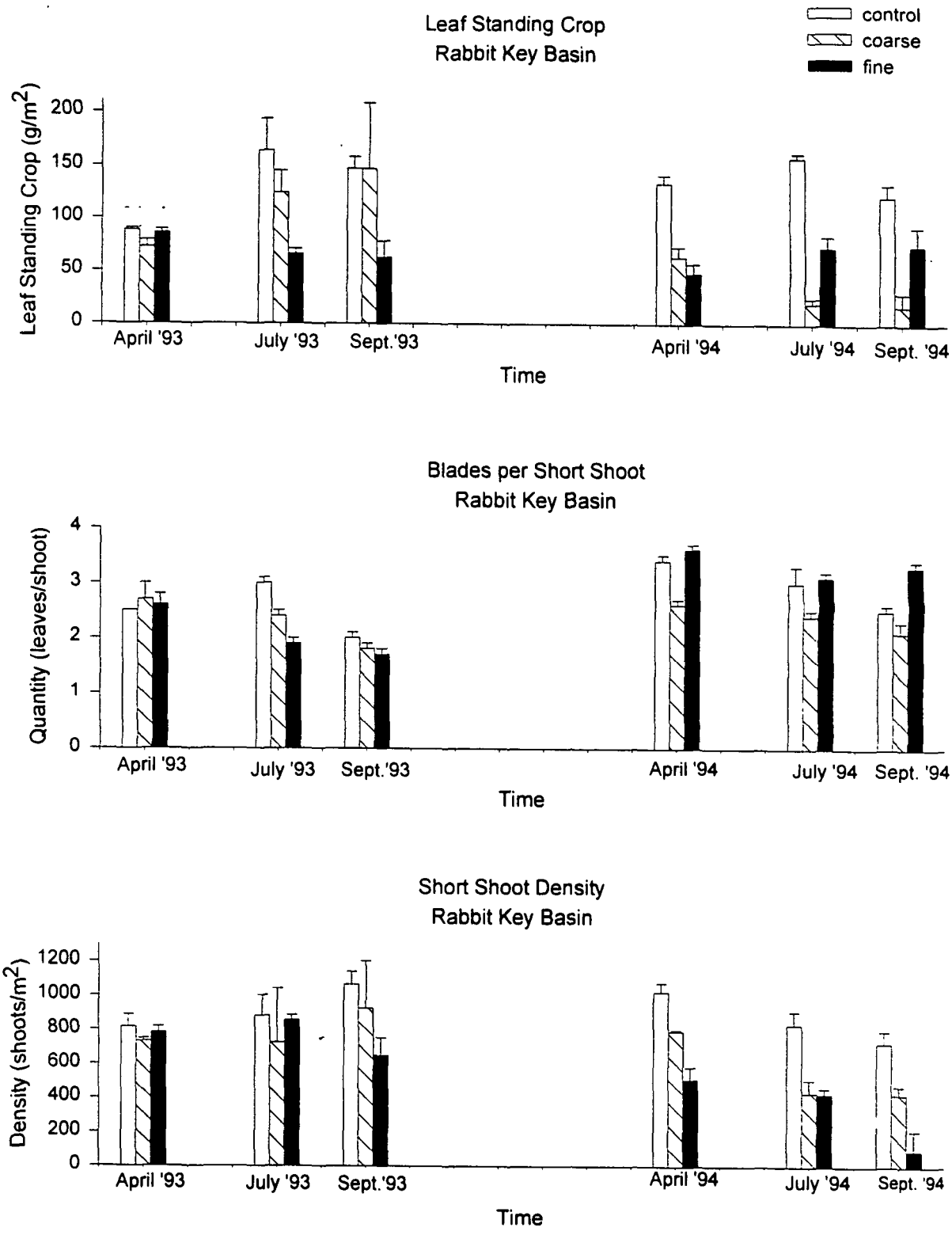


Fig. 3-7. Short shoot density (ss m^{-2}), leaves per short shoot (l ss^{-1}), and leaf standing crop (g m^{-2}) at Rabbit Key Basin.

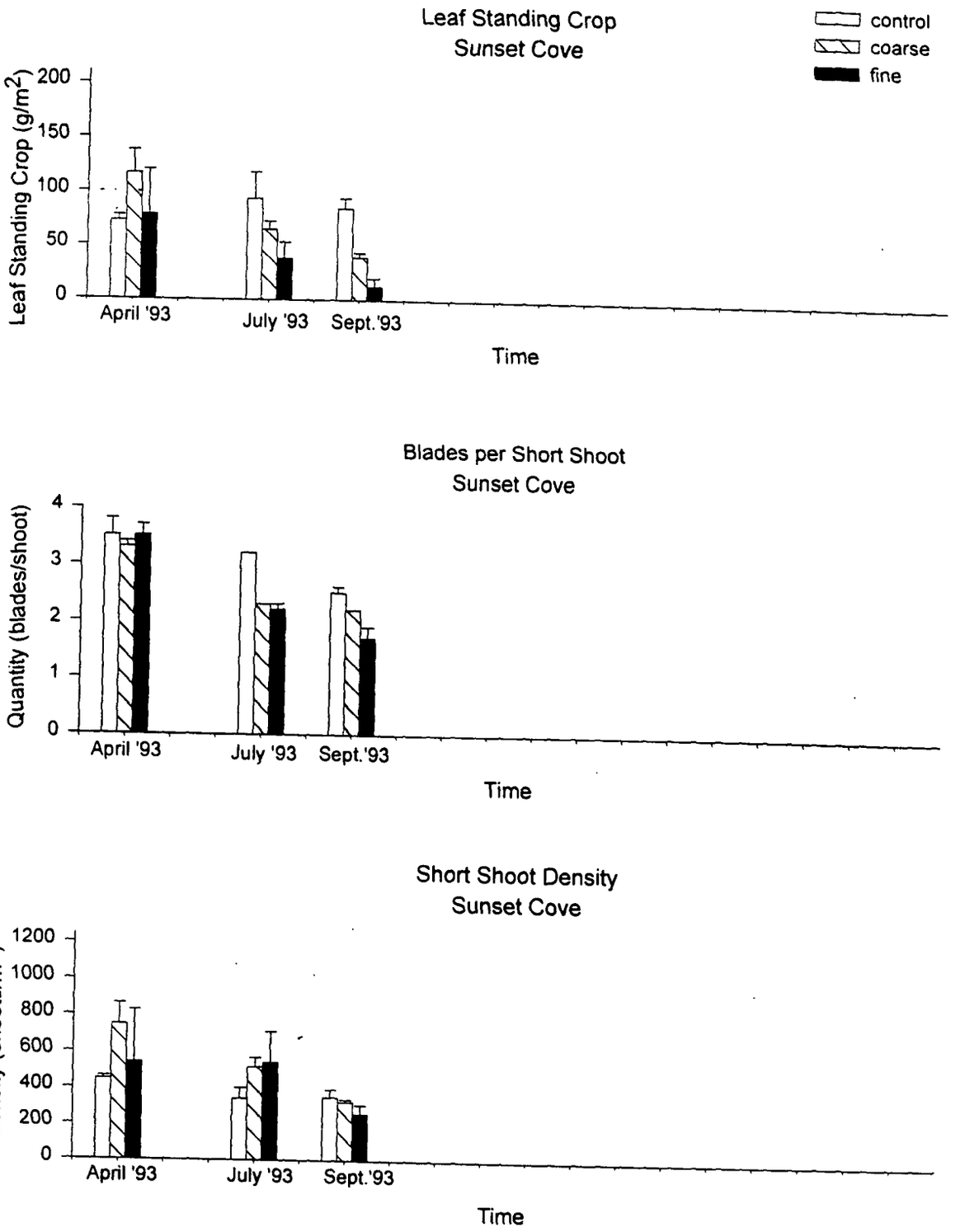


Fig. 3-8. Short shoot density (ss m^{-2}), leaves per short shoot (l ss^{-1}), and leaf standing crop (g m^{-2}) at Sunset Cove.

treatments showed a decrease relative to the control in July 1993. In September 1993 there was an increase in the standing crop at the coarse treatment, and it was equal to the control while the fine treatment continued at less than 50% of the control values. In 1994 the standing crop values in the coarse treatment declined to about 10 % of the control. Where the light reduction mesh had been removed the standing crop increased until it was greater than 50% of the amount of the control after having been much reduced. At both sites, this parameter showed one of the most direct and strongest responses to light reduction.

Photosynthetic Biomass In order to spread out the workload, the biomass samples were collected the month following the other biotic measurements. There was no biomass collected in March 1993. The photosynthetic biomass portion of the cored samples corresponds to the leaf standing crop, reported previously, but is from the biomass cores and therefore directly corresponds to the accompanying below ground biomass. At SUN there was an increase in photosynthetic biomass from the cores while the leaf standing crop reported no significant change. This is the only point on which the two methods of green plant estimates differ. The treatments showed significant decreases in photosynthetic biomass at the coarse treatment and a precipitous decline at the fine treatment. At RKB the patterning of all responses was nearly identical to that of leaf standing crop. The control plots showed a seasonal response pattern, the photosynthetic biomass from the coarse treatments declined throughout the project, and the fine treatment plots showed increases after the netting was removed.

Non-Photosynthetic Biomass. The nonphotosynthetic biomass at SUN showed little difference between control and the coarse mesh treatments over the duration of the experiment, but this fraction steadily declined in the fine mesh treatments. At RKB a seasonal effect was seen at all treatments, as was a persistent decline. By the end of the project, the non-photosynthetic biomass from the coarse mesh treatments was less than half of the control, while there was less decline in the recovering fine mesh treatments.

Total Biomass The total biomass of *Thalassia* is shown for completeness. Its behavior is primarily driven by that of the non-photosynthetic biomass.

Leaf Turnover Rate At SUN the turnover rates of *Thalassia* initially increased from April to July, but then declined in September. By September 1993, the treatment values had fallen below those of the control plots. At RKB leaf turnover rate was higher in 1994 than 1993, and was very consistent within each year. RKB showed a similar pattern to SUN in year one where initially the treatments were the same or higher than the control, but by the end of the year had declined to significantly less than the control. In 1994, the turnover rate of the control sites had increased, and the uncovered, former fine mesh treatments, increased similarly while the coarse mesh plots, while higher than in 1993, were less than the control values.

Areal Leaf Productivity At SUN the areal productivity at the control station increased in July and decreased by September. While the areal productivity at the coarse plots was significantly higher than the control initially, this fell off rapidly as the summer progressed. The areal productivity in the fine mesh cages decreased even more rapidly and was nearly zero by September 1993. The pattern of areal productivity at RKB for the control plots was similar in behavior to leaf turnover rate, with higher average values in 1994 than 1993. The areal productivity showed an immediate decline at both treatments relative to the controls, with significantly greater declines at the fine mesh stations. In 1994 areal productivity at the coarse mesh treatments continued a decline relative to the controls while the uncovered fine mesh plots increased to over 50% of the control values.

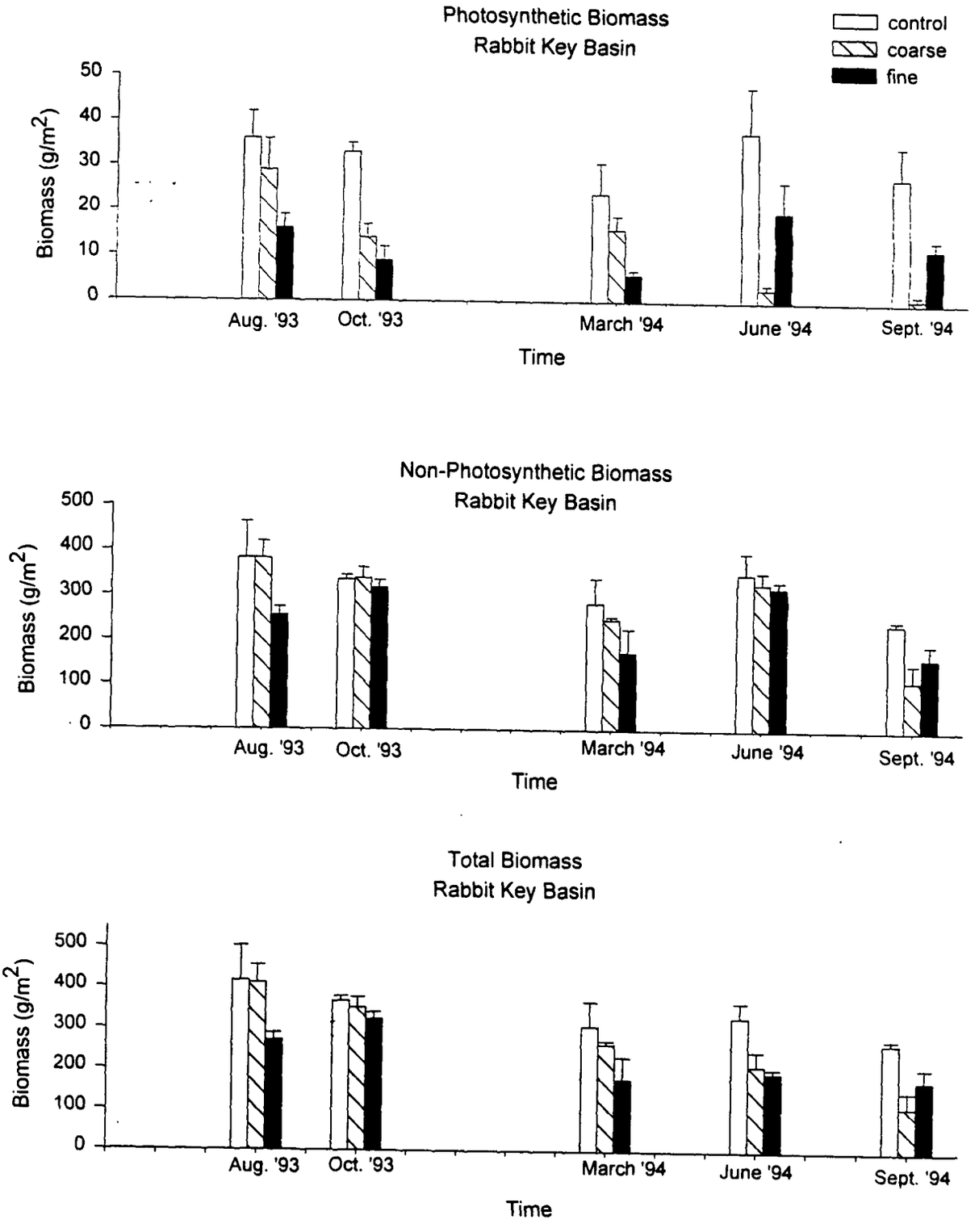


Fig. 3-9. Photosynthetic biomass (g m^{-2}), non-photosynthetic biomass (g m^{-2}), and total biomass (g m^{-2}) of *Thalassia* at Rabbit Key Basin.

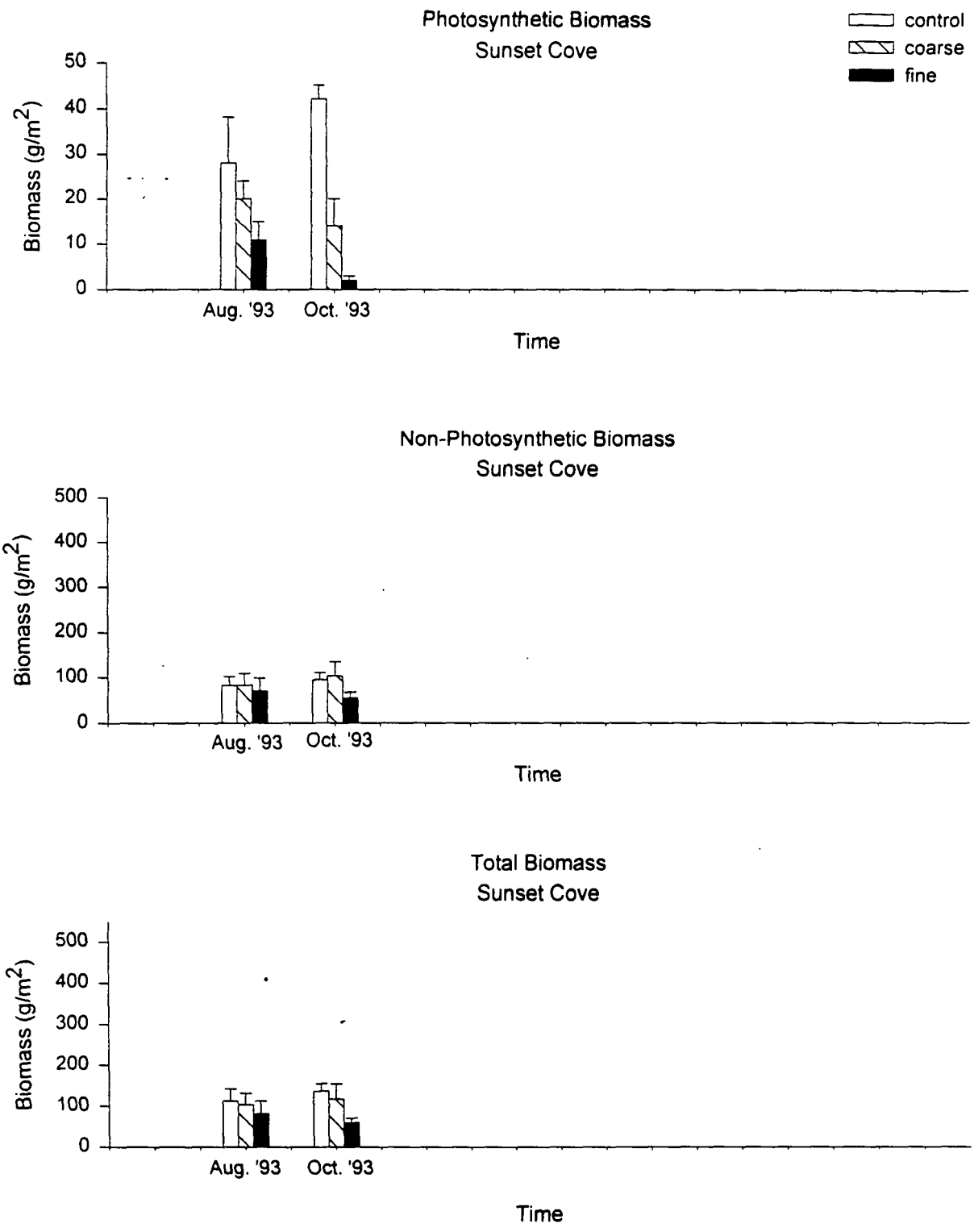


Fig. 3-10. Photosynthetic biomass (g m^{-2}), non-photosynthetic biomass (g m^{-2}), and total biomass (g m^{-2}) of *Thalassia* at Sunset Cove.

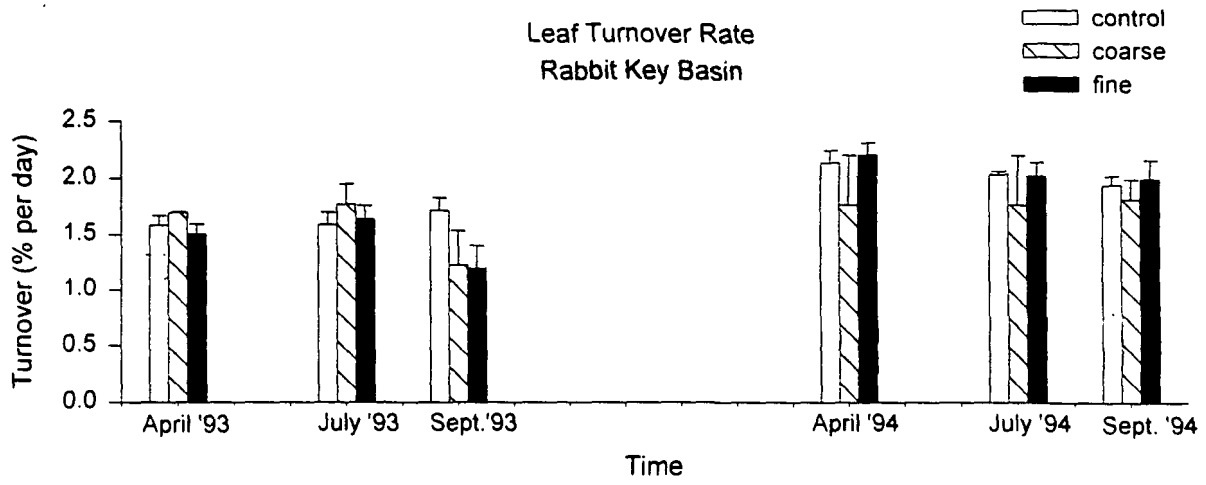
Photosynthetic to Non-Photosynthetic Biomass Ratio This is the ratio of photosynthetic to supporting tissue. Historically *Thalassia* from Florida Bay has had a low ratio, with green tissue being only 10-15% of the total plant biomass, and the high values seen at SUN are anomalously high for *Thalassia*. At the control plots the photosynthetic tissue ranged from 25 to 31% of the non-photosynthetic tissue. While these values are high, they declined rapidly with the stress of light reduction. The seagrass beds at SUN have developed to their 1987-1993 abundance in a relatively short time. It is believed that the trapping of rich nutrient material due to the physiographic shape of the cove, possibly coupled by enhanced nutrient runoff from development, has aided in developing an extremely rich bed that does not have the normal sediment development of the rest of Florida Bay, thus yielding the very high above/below ground ratios. By comparison with SUN, the ratios in RKB at the control plots are characteristic of Florida Bay, averaging about 10%. In 1993 the effects of the shading are seen to decrease the green tissue in both treatments, with greater decreases in the fine treatment. By 1994 the coarse treatment continues to decline, but the percentage of green tissue increases in the fine plots that have had their cages removed.

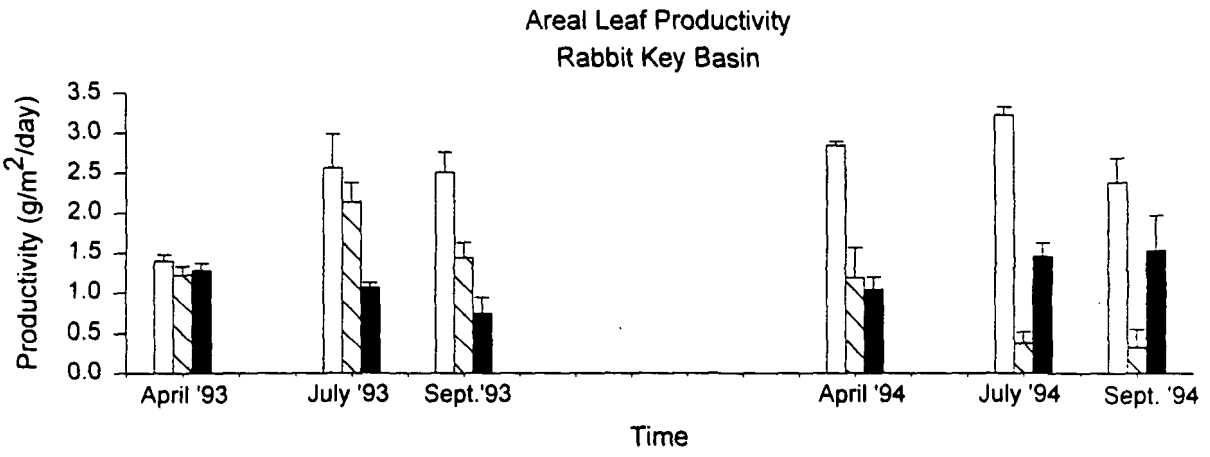
DISCUSSION

Physical parameters. Shortly after the cages were installed, integrated light readings showed that the coarse mesh cages were receiving about 50% of the light entering the control areas, while in the fine mesh cages the PAR was 30 % of the control. In the summer, PAR at the control sites increased from 20 to 30 mol photons m^{-2} d^{-1} (MPD), while the PAR in the experimental cages was, on the average, only slightly higher than initial values (Fig. 3-3). Throughout the first summer and fall the coarse treatments received 49 % of the MPD as the controls and the fine treatment 21%. In the winter months, the PAR in the control cages fell to roughly 50% of summer values while the PAR in the coarse mesh treatments declined by slightly less than 50%. Thus from beginning in May 1993 until March 1994, the coarse treatments were receiving around 50% of the PAR in the controls. By March 1994, PAR began to increase to summer values in the control, but there was little increase in the experimental plots at this time so that by the summer of 1994 the experimental treatments were receiving only about 30% of that of the control plots. Over the course of the entire experiment the coarse treatments received 43% of the MPD of the controls.

At the end of the previous decade, from 1986 thru 1988 especially, Florida Bay was an exceedingly stressful environment for seagrasses with salinities in the north-central core of the bay reaching 72 psu for several months and exceeding 50 psu for over 14 months. From long-term records, the summer and fall of 1987 was exceptionally hot and the waters were abnormally warm. In the late summer and fall of 1987 the beginnings were detected of the Florida Bay seagrass dieoff which has led to the loss of many thousands of hectares of seagrass. In addition the late summer of 1987, with its hot water, saw the largest coral bleaching event to date in the Florida Keys. Robblee et al (1991) documented a total loss of over 4,000 ha and extensive damage and loss to an additional 23,000 ha. This number has subsequently increased many times, but there is no currently accurate assessment of the extent, due in large part to persistent algal blooms and turbidity plumes.

By comparison with the physical conditions in the late 1980's, the 1993-1994 time period were relatively benign. The greatest apparent physical stressor during the time of the experiments would have most likely been temperature and not salinity. Temperatures were quite warm in the summer of 1993, exceeding 30°C from July to September (Fig. 3-4). 1994 saw lower temperatures in the summer, and the temperature data correlated well with the PAR data, which also showed both higher average MPD and a longer duration of higher MPD in the summer of 1993 than in 1994. Note that this does not correlate with the absolute highest PAR intensity. A comparison of figures 3-2 and 3-3 shows that while the highest integrated photon flux values occurred in the summer of 1993, the highest intensities occurred in March of 1994.





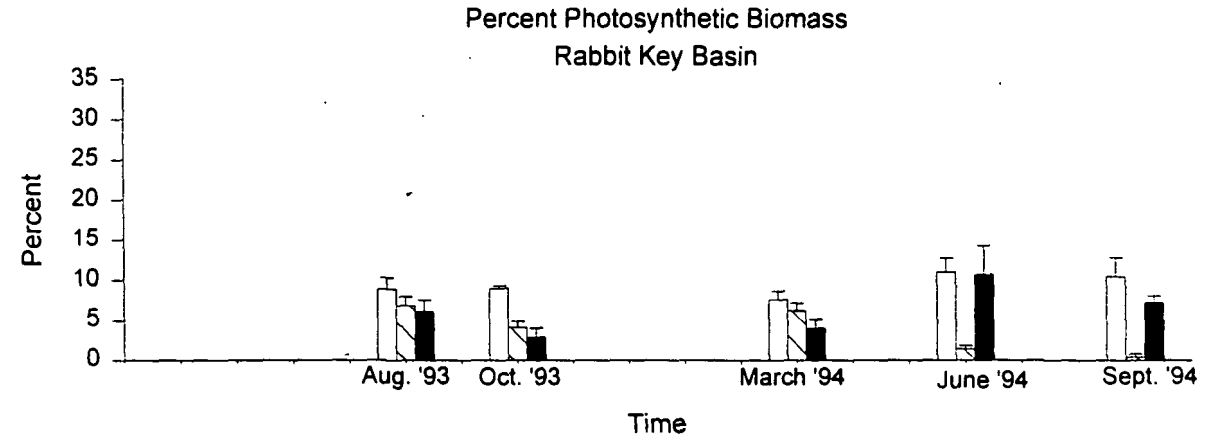


Fig. 3-11. Turnover rate (% d^{-1}), areal productivity (g m^{-2} d^{-1}), and the ratio of photosynthetic to non-photosynthetic biomass (%) of *Thalassia* at Rabbit Key Basin.

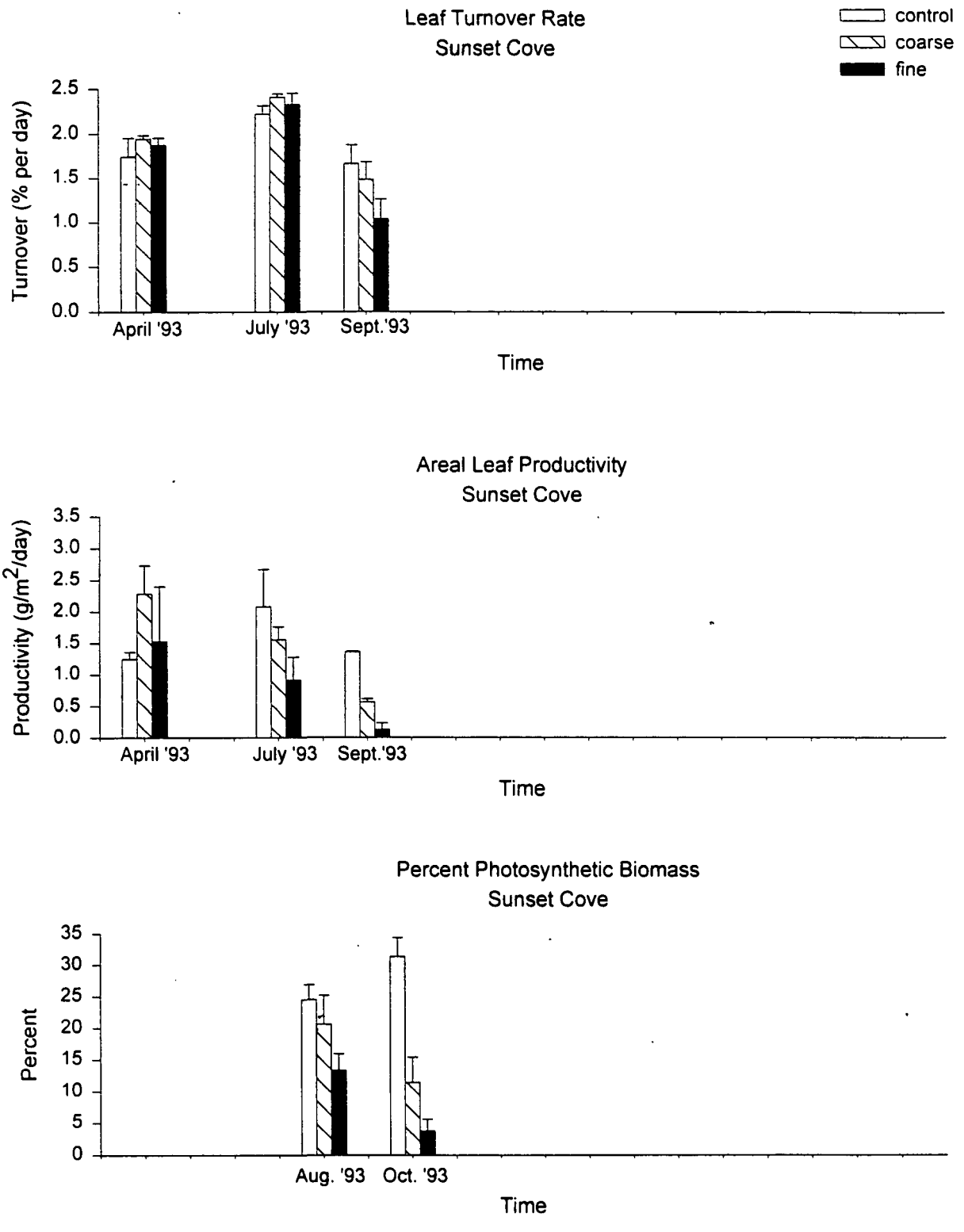


Fig. 3-12. Turnover rate (% d^{-1}), areal productivity (g m^{-2} d^{-1}), and the ratio of photosynthetic to non-photosynthetic biomass (%) of *Thalassia* at Sunset Cove.

Salinities throughout the experimental period were near seawater strength for both stations. RKB was nearly constant at 36-37 psu, while SUN varied from 28-38 during the time of the experiment there. Neither of these salinity regimes should have been a significant source of stress to *Thalassia*, although the variations may well have caused some of the differential responses seen between the years 1993 and 1994.

Biotic Parameters At the beginning of the experiment, the standing crop in RKB averaged 82 $g \cdot m^2$ and SUN averaged 89 $g \cdot m^2$. In 1983-84 the bay-wide average for *Thalassia* was 67 $g \cdot m^2$ (Zieman et al 1989). While the initial values for these stations are somewhat higher than the bay-wide average, they are typical of the specific habitats involved. While the responses of the control plots are seen to be within normal variation in the fall samplings (comparison of September 1993 with September 1994), the progressive loss of standing crop in the coarse mesh treatment after year 1 shows the effects of the long-term light reduction. The pattern at SUN was essentially the same. The following discussion will be based mostly on the RKB station because of its longer data base, but note will be given where the behaviors differ significantly. Comparing September 1993 with 1994, the control plots lost about 13 % of their standing crop while the coarse mesh plots lost 78%, a very significant loss. The fine mesh cages showed a greater rate of decrease while under treatment, and rebounded somewhat following shade removal.

This pattern is mirrored with the LAI response, as LAI is a parameter that is closely coupled with standing crop. What is instructive is analyzing how these changes are produced. Leaf width showed virtually *no* change at the control plot or the fine mesh treatments, but did progressively decrease in the coarse mesh treatments. Decreasing leaf width has been shown to be a parameter that is sensitive to stress in seagrasses. The *Thalassia* leaves at the control site increased in length throughout the experiment. In the coarse treatment the leaf length increased initially but then declined to a length that was similar to that at the start of the experiment. The number of leaves per short shoot tended to vary similarly across all treatments, but the short shoot density showed very pronounced behavior. At the control plots, the short shoot density increased in the middle of the experiment, but by the end was similar to the density at the beginning. There was some initial increase in short shoot density in the coarse treatment plots, but in 1994 these showed a strong progressive decline so that by September 1994 they were over 30% less than the densities in the control plots. Compared with most other parameters measured, the short shoot density, which had declined by the fall of 1993, continued to decline even after the screening was removed in the fine mesh plots.

At the control site, the leaves maintained their standing crop and LAI by becoming longer and slightly wider as the short shoot density declined slightly. This may be a response of the plant to produce larger, and especially longer leaves in response to a better light field. All of these parameters declined in the coarse treatments resulting in the great decline in standing crop and LAI seen there. While the short shoot density continued to decline in the fine treatment plots, the plants responded with longer, wider leaves and increased the number of leaves per short shoot by 50%.

Throughout the experiment, the pattern of photosynthetic biomass from plants from core samples showed very similar response to leaf standing crop from the productivity samples. This was similar across all treatments. During this time there was somewhat of a decrease in total biomass, which was generated by the change in below ground biomass. By the end of the experiment, the total biomass in the coarse mesh treatment was less than 50% of the controls, while the former fine treatments were only about 30 % less. The result of these changes is best illustrated in the ratio of photosynthetic to non-photosynthetic biomass. This parameter shows a slight increase throughout time at the controls, declines greatly in the coarse mesh treatment and declines and then rebounds at the fine treatments.

The major differences in the responses between RKB and SUN were brought about by the greatly reduced belowground biomass at SUN. While the non-photosynthetic biomass at RKB decreased from 1993 to 1994, the same fraction at SUN was only 25-30% of the amount at RKB. For Florida Bay, the ratios found at RKB are much more typical of the system than those at SUN. It is believed that this is the result of rapid expansion into a very nutrient rich environment at SUN. This appears to be a combination of natural trapping of sediments

by the physiographic makeup of the site, with the potential of nutrient input from lawns and nearby development.

The turnover rate is a measure of the dynamic performance of the plant. It is produced dividing the areal productivity by the standing crop. As the number is then normalized, it is a useful measure to compare seagrass meadows that vary greatly in biomass. While the turnover rate for localities tends to be consistent over time, there were major differences in all treatments between 1993 and 1994. At the control plots the turnover rate (here expressed as % d^{-1}) was 1-6-1.7 % d^{-1} in 1993 and near 2 % d^{-1} in 1994. By September 1993, the treatment rates had declined relative to the control. In 1994, the coarse mesh treatment remained lower than the control, but the former fine mesh plots rebounded and were growing at a rate equal to the controls.

IV ST. JOSEPH'S BAY, FLORIDA, SITE

Cynthia A. Moncreiff, Kenneth L. Heck, Jr., Jill M. Zande

MATERIALS AND METHODS

Study area. St. Joseph Bay, located in the northeastern Gulf of Mexico, is a protected, shallow coastal embayment with extensive seagrass habitat dominated by monospecific stands of *Thalassia testudinum* Banks ex König (Iverson and Bittaker 1986). The study site selected for light manipulations was located on the west side of St. Joseph Bay near Eagle Harbor (29°46'N, 85°24'W) (Fig. 4-1). This embayment has no significant sources of freshwater input (Valentine and Heck 1991) other than local rainfall. Mean tidal range is approximately 0.4 m, with a daily to mixed frequency; local winds often overwhelm this microtidal regime (Tide1 Tide Prediction Software 1995). Salinity varied from 26 to 38‰ and temperature from 6.5 to 33°C over the course of the study; these values were slightly outside of the reported ranges of 30 to 36‰ for salinity and 8 to 30°C for temperature (Valentine and Heck 1991). Peak production rates for seagrasses are reported to be nearly 75 g C m^{-2} y^{-1} (Iverson and Bittaker 1986). The site is relatively pristine, with minimal influences from industrial development and limited commercial fishing activities; the area is a component of the T. H. Stone Memorial St. Joseph Peninsula State Park. Nutrient, suspended sediment, and particulate organic matter levels are generally low; water clarity is high, with visibility generally well in excess of 2 m (6.6 ft). Water in St. Joseph Bay has a history of being quite clear, due in large part to the coarse sand sediments in the bay (Iverson and Bittaker 1986)

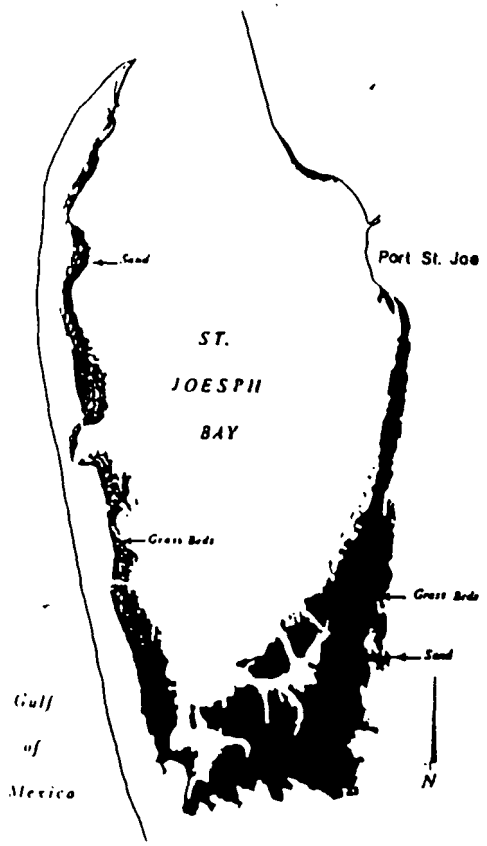


Fig. 4-1. Map showing study area location in the northeastern Gulf of Mexico on the west shore of St. Joseph Bay.

Experimental design. A series of enclosures, constructed of a 1.75 m x 1.75 m (5.7 ft) x 0.6 m (2 ft) height schedule 40 PVC frame covered with neutral density plastic mesh (extruded Vexar Diamond mesh, Internet, Inc., Minneapolis, MN) secured to the frame with cable ties, were designed so that the tops could be removed for sampling and enclosure maintenance. Two different mesh sizes (fine and coarse) were used to achieve the desired light level reductions: 6.4 mm (1/4") mesh (fine), which resulted in a reduction to 30-40% of surface irradiance; and 19.4 mm (3/4") mesh (coarse), which produced a reduction to 60-70% of surface irradiance. Control enclosures (no reduction) were used to assess any potential caging effects. Mist netting was used to cover the tops of the enclosures for the purpose of exclusion of the short-spined sea urchin, *Lytechinus variegatus* (Lamarck), from the enclosures, as sea urchin herbivory has been demonstrated to affect seagrass growth responses (Valentine and Heck 1991). Three replicate enclosures were constructed for each treatment for a total of 9 enclosures.

The enclosures were placed in a continuous bed of *Thalassia testudinum* with an average depth of 1 m and secured to the substrate; the perimeters of each enclosure were cut to a depth below the rhizome layer (approx. 40 cm) to ensure the separation of the plants from the rest of the meadow with respect to physiological resources (Tomasko and Dawes 1989). Enclosures were cleaned every two weeks or as needed to control epibionts; this was critical as any great degree of growth of material on the neutral density plastic mesh had a measurable effect on transmittance and attenuation of light reaching the enclosed seagrasses. Enclosure tops were removed during this process to ensure complete cleaning and to minimize the impact of adding epibiont material to the enclosures.

Sampling schedule and design. Enclosures were deployed on 20 March 1993; initial samples were collected from within each enclosure area on 21 March, and pore water sulfide collected on 24 March. The remaining quarterly samplings were conducted on 11-12 June and 25-26 September 1993. Short shoots of *Thalassia* marked using a modification of Zieman's (1974) leaf marking technique were harvested no more than 3 weeks post-marking. During the first year of the study, samples were collected as described in the original protocol, with the modifications detailed below.

RESULTS

Light. As stated earlier, the enclosures produced reductions in light levels reaching the seagrass canopy at the site of 60-70% of that normally reaching these submerged plants within the 19 mm (3/4") mesh enclosures (reduction to 60-70% ambient light), and a reduction to only 30-40% of normal light levels with the 6.4 mm (1/4") mesh (reduction to 30-40% ambient light). Actual measured light levels representative of what was observed throughout the study are shown in Table 4-1. Degree of light attenuation varied as a result of levels of epibiont accumulation on the enclosures used to shade the seagrass. Light levels at times approached the hypothetical minimum of 10% of surface irradiance required to support the growth of *Thalassia testudinum* (Iverson and

Date	Enclosure	Surface irradiance	Light reaching enclosed canopy
24-VII-93	Control	2800	1033 ± 115
	Coarse (3/4")	2766	740 ± 40
	Fine (1/4")	2667	467 ± 24
6-X-94	Control	2360	563 ± 23
	Coarse (3/4")	2367	240 ± 20
	Recovery (former 1/4")		

Table 4-1. Typical observed light reductions at St. Joseph Bay study site. Values shown are expressed in $\mu E\ m^{-2}\ s^{-1}$.

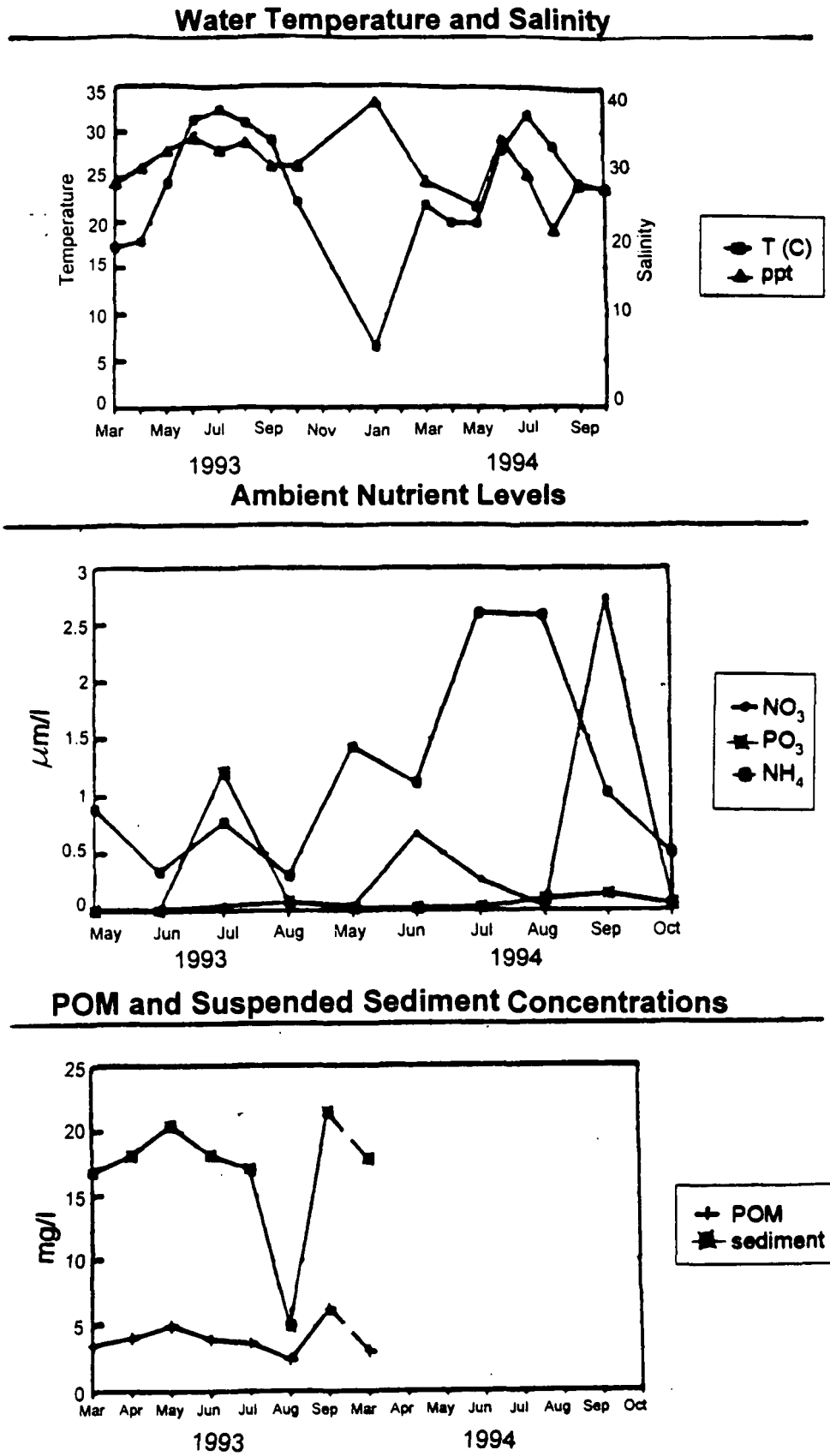


Fig. 4-2. Water temperature, salinity, ambient nutrient levels, suspended sediments, and particulate organic matter (POM) at the St. Joseph Bay study site.

Bittaker 1986). Another consideration is the wavelengths of PAR reaching the substrate; Calem and Pierce (1993) found that distribution of *T. testudinum* was limited to areas where blue light reached the sediment surface. Light attenuation by the Vexar mesh, especially when heavily epiphytized, may have potentially affected this parameter. Other physical and chemical parameters. Water temperature, salinity, and ambient nutrient levels are shown graphically in figure 4-2. Temperature ranged from a low of 6.5°C in January 1994 to a high of 33°C, observed in July of both years of the study. Salinity ranged from a low of 19 ppt following an intense local rainfall event in August 1994 to a high of 38 ppt in January, which coincided with the observed temperature minimum. Nutrient levels were consistently low over the course of the study; NO_3 ranged from 0.03 to 2.73 µm/l, PO_4 from 0.02 to 0.14 µm/l, and NH_4 from 0.5 to 2.58 µm/l. Suspended sediment and POM levels were also consistently low, with suspended sediment concentrations generally averaging less than 20 mg/l and POM less than 5 mg/l dry weight. Lower values were observed during the calmest observed field conditions.

Thalassia response. Plant response parameters are shown graphically in figures 4-3 through 4-6. Standing crop of *Thalassia testudinum* showed expected seasonal trends, with lowest values being observed in March 1994 prior to the onset of spring growth. A significantly lower standing crop was observed in September 1993 for the 6.4 mm (1/4") mesh treatment ($p<0.05$). A similar pattern was observed in areal leaf production (Fig. 4-3) and in leaf area index (Fig. 4-4). Turnover rates (Fig. 4.3) were lowest in September 1993 for all treatments. The zero value observed for the 6.4 mm (1/4") mesh treatment in March 1994 was due to complete grazing of all marked shoots within the enclosures by rogue sea urchins. Compensatory growth appeared to be occurring in the shaded and recovery treatments in September 1994, with the 6.4 mm (1/4") mesh turnover rate being significantly different from the control ($P<0.05$).

Urchin grazing of marked shoots in March 1994 resulted in zero values for leaf area index (LAI) (Fig. 4-4). LAI was significantly reduced in the 1/4 mesh treatment in both June and September 1993 ($P<0.05$); differences at all other times were not significant. During the 1994 recovery phase for the 6.4 mm (1/4") mesh treatment, LAI returned to pre-shading levels.

Average seagrass blade widths showed a trend towards a decrease in response to shading; however, differences among treatments were significant only in March 1994 ($p<0.05$); the recovering 6.4 mm (1/4") mesh treatment was different from the control ($p<0.05$). Total plant biomass (Fig. 4-4) was highest in all treatments at the initiation of the study, and showed a decrease from March to June that may have been a result of severing rhizomes to eliminate contributions to the enclosed plant material from outside the enclosures. Total biomass remained relatively constant throughout the remainder of the study. Rhizome and root biomass (Fig. 4-5.) showed similar trends. Above- to below-ground biomass ratios were lowest in March of both years of the study, with the zero value observed in the recovering 6.4 mm (1/4") mesh treatment resulting from nearly complete grazing of aboveground biomass by urchins. This ratio was markedly higher in control treatments in June of both years, and sufficiently higher in June 1994 to suggest that a shading response was beginning to occur in the 19 mm (3/4") mesh treatment.

Short shoot densities (Fig. 4-6) were significantly lower in the 6.4 mm (1/4") mesh treatment in September 1993 in comparison the control and 19 mm (3/4") mesh treatments ($P<0.05$), and also throughout 1994. Shoot specific growth rates were significantly depressed in the 6.4 mm (1/4") mesh treatment in September 1993 and in June 1994 relative to the control. Additional evidence for compensatory growth during the recovery phase for this treatment is suggested by the high rate observed in September 1994.

Calcareous epibiont coverage was examined only at the St. Joseph Bay site due to problems with spontaneous separation of epiphytes from leaves during shipment of samples from the other sites (Corpus Christi Bay, Texas and Florida Bay, Florida). This information is shown in figure 4-6. There appear to be fewer encrusting organisms present on seagrass blades during June of both years. Differences among treatments were not significant.

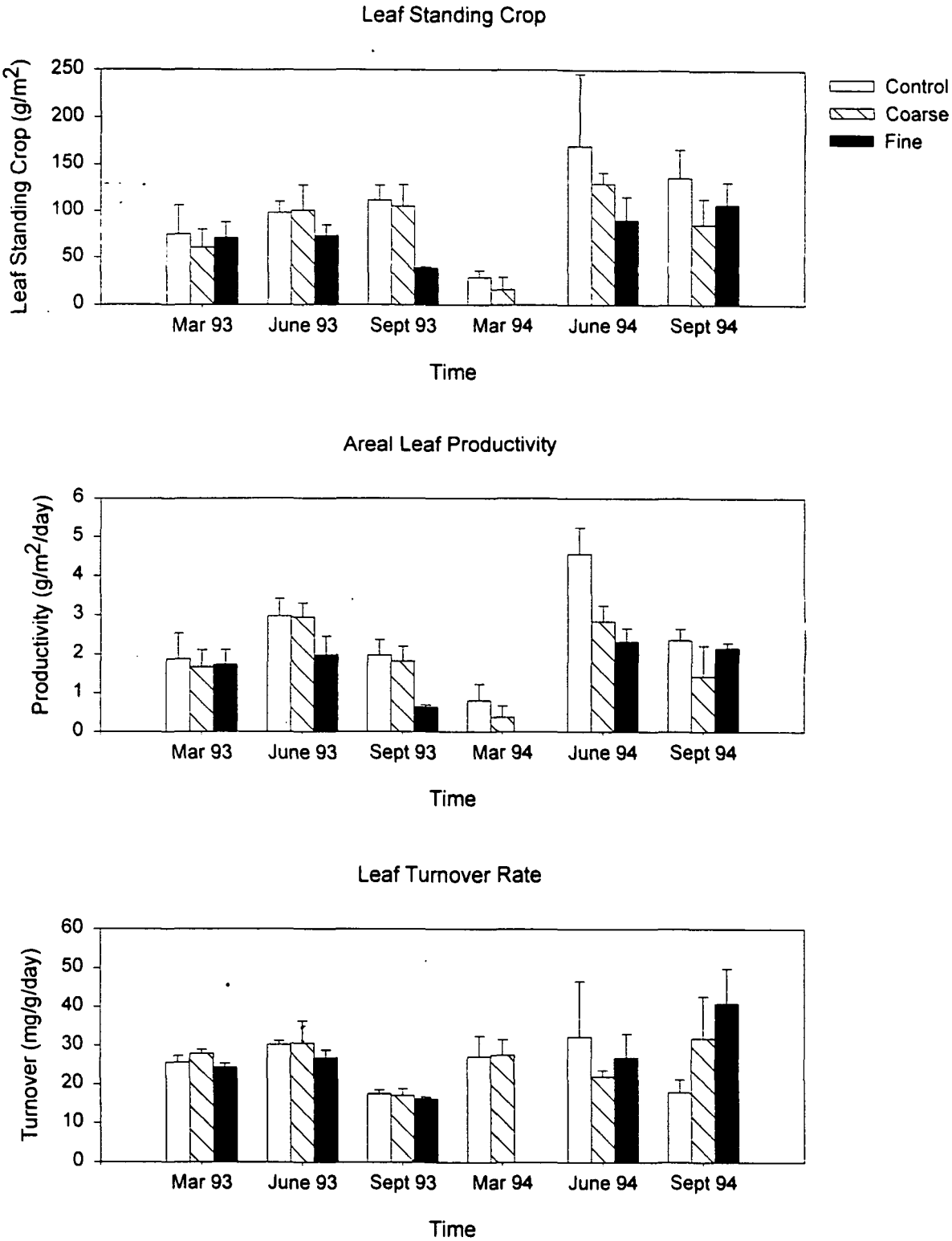


Fig. 4-3. Standing crop (g m^{-2}), biomass productivity (g m^{-2} d^{-1}), and turnover rate (mg g^{-1} d^{-1}) for *Thalassia testudinum* at the St. Joseph Bay study site.

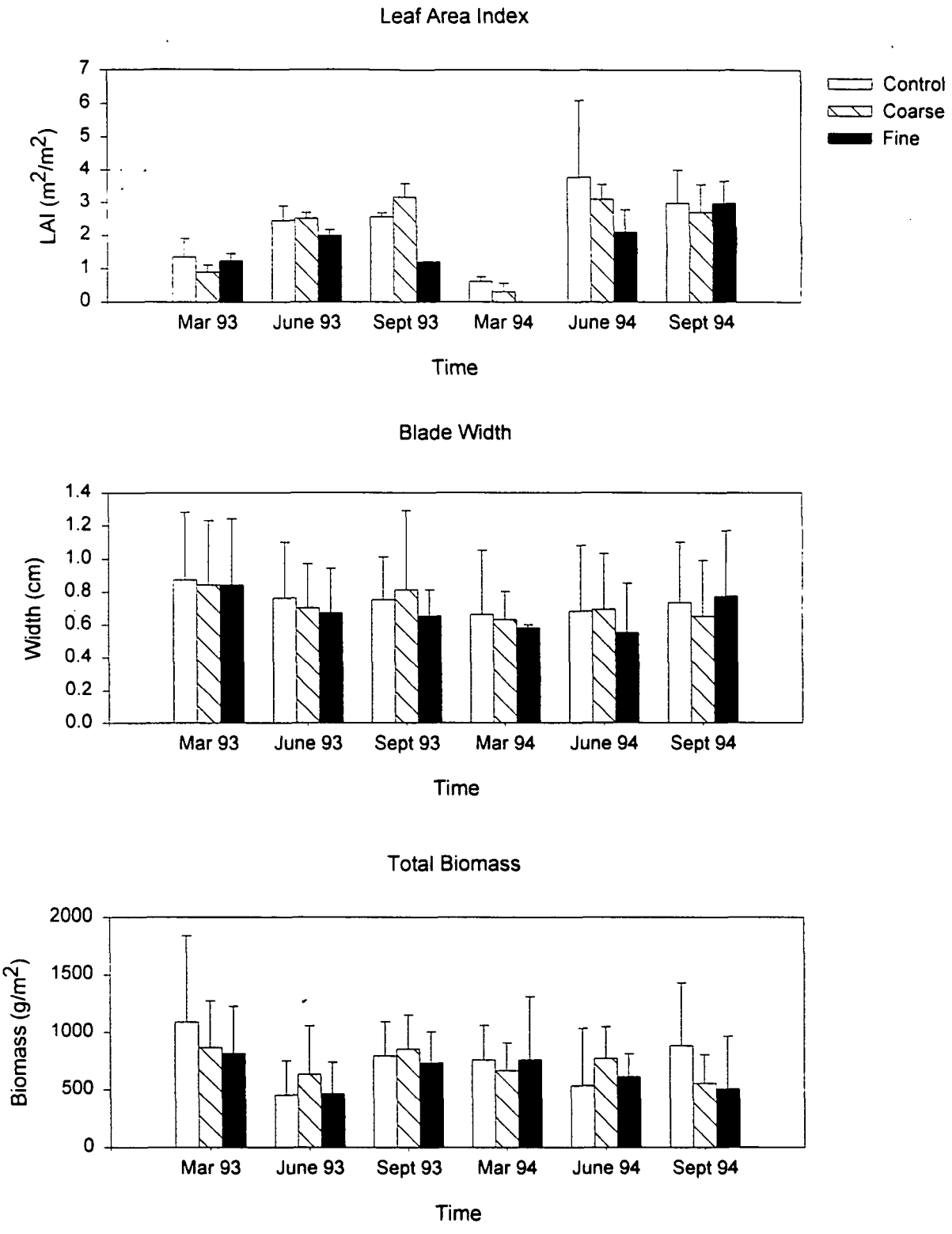


Fig. 4-4. Leaf area index (LAI, m^2/m^2), blade width (cm), and total biomass ($g\ m^{-2}$) for *Thalassia testudinum* at the St. Joseph Bay study site.

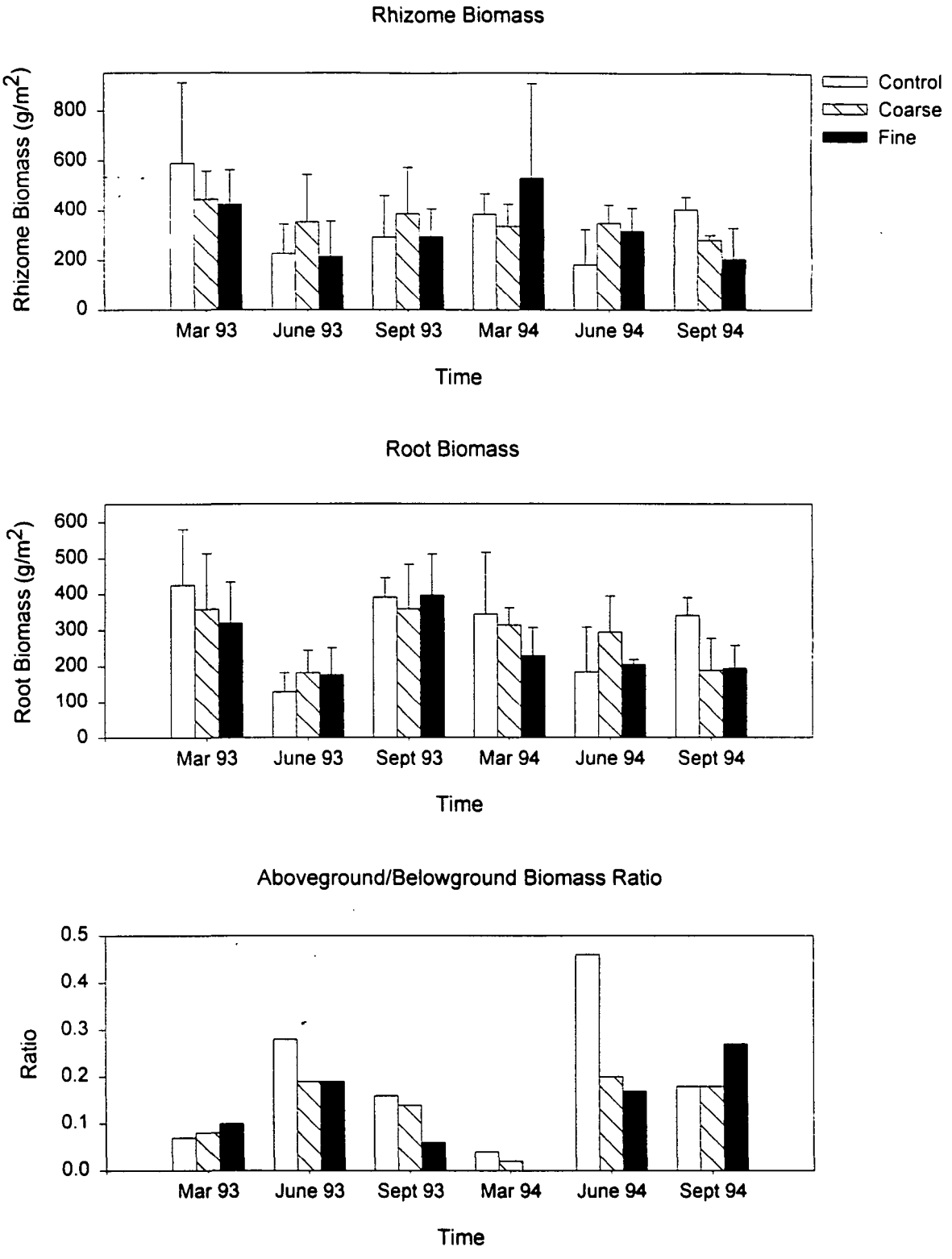


Fig. 4-5. Rhizome biomass (g m^{-2}), root biomass (g m^{-2}), and above-to below-ground biomass ratio for *Thalassia testudinum* at the St. Joseph Bay study site.

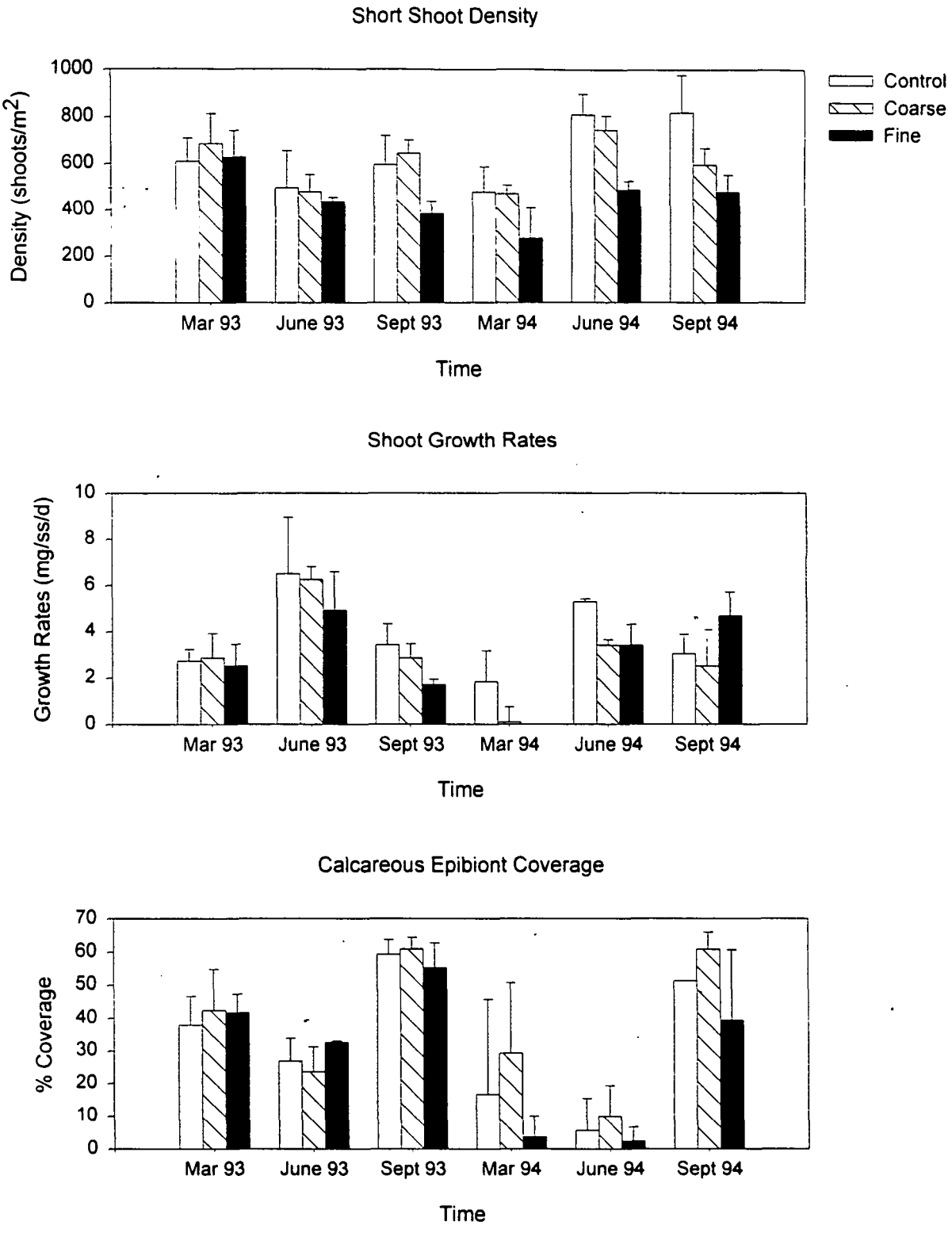


Fig. 4-6. Short shoot densities (m^{-2}), shoot specific growth rates (g ss^{-1} d^{-1}), and calcareous epibiont coverage for *Thalassia testudinum* at the St. Joseph Bay study site.

Mesograzer abundances were also examined only at the St. Joseph Bay site due to problems with shipment of samples from the other sites (Corpus Christi Bay, Texas and Florida Bay, Florida). These samples were sorted and the organisms found identified within a series of functional groups. As for the calcareous epibionts, there appeared to be fewer organisms present among the seagrass blades during the second year of the study, likely as a result of decreased short shoot densities. There may also have been some enclosure effects, but they were not detected. Differences among treatments were not significant.

DISCUSSION

The primary purpose of this study was to examine the response of *Thalassia testudinum* to chronic reductions in light. Seagrasses have the potential to respond to light reductions in a number of ways, and exhibit a wide range of growth responses on both seasonal and annual scales (Zieman and Zieman 1993, Marba et al. 1994); these variations must be considered when interpreting observed results. Previous studies have indicated that stunted growth, decreased short shoot densities, and reduced biomass were common responses, and that light levels equivalent to 20% of surface irradiance were necessary for continued seagrass survival (Short et al. 1974, Congdon and McComb 1979, Dennison 1987, Kenworthy and Haunert 1991). The findings of this study appear to support these observations.

Light. As explained previously, the enclosures produced reductions in light levels reaching the seagrass canopy of 60-70% within the 19 mm (3/4") mesh enclosures, and a reduction to only 30-40% of normal light levels with the 6.4 mm (1/4") mesh enclosures. Actual measured light levels at times approached the hypothetical minimum of 10% of surface irradiance required to support the growth of *Thalassia testudinum* (Iverson and Bittaker 1986). Based on observed plant responses in the 6.4 mm (1/4") mesh treatment, reduction in light to levels that are 30-40% of normal ambient light were sufficient to significantly suppress growth to a level that was not tolerated by *T. testudinum*. Olesen and Sand-Jensen (1993) observed that zero growth occurred in *Zostera marina* at 11% of surface photosynthetically active radiation (PAR); the shading in this study approximated delivery of 15% of surface PAR with the 6.4 mm (1/4") mesh treatment for a growth response close to zero. However, by removing the shading stress during the second year of the study, we demonstrated that in St. Joseph Bay, the plants were able to recover within less than one year to pre-stress conditions.

Other physical and chemical parameters. Water temperature and salinity were generally within the optimal ranges reported elsewhere for *Thalassia testudinum* (Phillips 1960). Suspended sediment and POM levels were also consistent with suspended sediment concentrations generally considered acceptable for submerged aquatic vegetation (Dennison et al. 1993). Macauley and others (1988) found that *T. testudinum* responded most strongly to water temperature, although light is often thought to be a more critical parameter (Iverson and Bittaker 1986, Robblee et al. 1991).

***Thalassia* response.** Values observed for short shoot densities and standing crop (aboveground biomass) of *Thalassia testudinum* in Gulf of Mexico seagrass beds are shown in Table 4-2 for purposes of comparison with the present study. Observed values for control enclosures fell well within the range observed for other studies in northern Gulf of Mexico seagrass meadows. Iverson and Bittaker (1986) reported short shoot densities of roughly 600 m^{-2} in April to 1100 m^{-2} in September; observed values for all treatments were closer to the value reported in their study for April. However, they indicate that short shoot numbers were relatively constant in St. Joseph Bay, which was observed in all but the 6.4 mm (1/4") mesh treatment.

Compensatory growth which appeared to occur in both the shaded 19 mm (3/4") mesh and recovery treatments in September 1994 is consistent with plant responses to shading reported in the literature (Olesen and Sand-Jensen 1993, Gordon et al. 1994). However, use of leaf marking as a technique to monitor plant response in shading studies is perhaps inappropriate. Leaf elongation occurs in response to reduced light levels, which can give a false indication of plant response when assessing growth energetics (Olesen and Sand-Jensen 1993; Czerny and Dunton 1995).

Location	Short Shoots m^{-2}	g dry wt m^{-2}	Reference
Edmont Key, FL 1981	505	---	Durako and Moffler 1987
1982	788	---	
1983	560	---	
1985	500	---	
Perdido Key, FL 1993	684	82.3	Heck et al. 1994
1994	825	49.5	
Boca Ciega Bay, FL	---	480	Taylor et al. 1973
St. Joseph Bay, FL	200	---	Valentine and Heck 1991
St. Joseph Bay, FL	564	94.9	This study
1994	700	111.5	

Table 4-2. Short shoot densities and aboveground biomass of *Thalassia testudinum* beds in Gulf of Mexico seagrass studies.

Observed above- to below-ground biomass ratios were somewhat different than responses seen in other seagrass species. In *Zostera marina*, more biomass was apportioned to leaves than to rhizomes with reduced light, resulting in an increase in this ratio (Olesen and Sand-Jensen 1993). This ratio was only observed to increase in this study in the control treatment, primarily as a seasonal growth response.

Short shoot densities were lower for both shade treatments at the conclusion of the study, even though the 6.4 mm (1/4") mesh treatment was allowed to recover. Similar results have been observed for *Posidonia sinuosa* following a 5-month period of intense shading ($\geq$ 80% light reduction; Gordon et al. 1994). This response is also significant in light of the relative constant short shoot densities observed over time in St. Joseph Bay (Iverson and Bittaker 1986; this study).

Calcareous epibiont growth on seagrass blades was anticipated to respond to changes in leaf elongation rates and to short shoot growth rates, in general, with epibiont load increasing in the shaded treatments over time in response to eventual slower growth rates. Although decreased shoot specific growth rates were observed, an increase in epibiont coverage was not. Lower percent coverage of leaf surfaces was observed in the 6.4 mm (1/4") mesh treatment throughout 1994, although it was not statistically significant due to large standard errors in this parameter. Differences may have resulted from the decreased availability of colonizing organisms in the 6.4 mm (1/4") mesh treatments in conjunction with decreased numbers of short shoots in these enclosures, even during the recovery phase or decreased growth of epibiont due to shading.

As stated earlier, mesograzer abundances were determined on the basis of functional groups. It was expected that the mesograzer community would respond to decreases in seagrass biomass and decreased short shoot densities as observed in other studies (Connolly 1995). As for the calcareous epibionts, there appeared to be fewer organisms present among the seagrass blades during the second year of the study, likely as a result of decreased short shoot densities. There may also have been some enclosure effects, but they were not detected.

Results of this study indicate that *Thalassia testudinum* meadows in St. Joseph Bay, which are presently not impacted by chronic reduced light levels or other physicochemical stresses such as high sulfide levels or

reduced salinities, have a high potential for use in future studies of reductions in light that are more subtle than that achieved with the 6.4 mm (1/4") mesh treatments. Observations of plant responses to longer-term reductions in light than those observed in this study will provide the type of information that will allow the questions resulting from observed cause-and-effect relationships among the environmental parameters that potentially can affect the survival and growth of seagrasses in critical coastal habitats.

V. CORPUS CHRISTI BAY, TEXAS

Kun-Seop Lee and Kenneth H. Dunton

MATERIALS AND METHODS

Study Site The study site is located in eastern side of Corpus Christi Bay (27° 49' N, 97° 7' W). This site has been the focus of several recent investigations on south Texas seagrasses (Dunton, 1990, 1994; Czerny & Dunton, 1995). *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme* are the dominant seagrass species in this area. This study was conducted on a monotypic meadow of *Thalassia testudinum* with an average water depth of 1.2 m. Water temperature ranged from 34°C in July and August to 13°C in January, while salinity varied from 27 to 32 ‰.

In situ Light Manipulation Light shading cages (1.5m x 1.5m x 0.5m) were placed in a monotypic meadow of *Thalassia testudinum* to achieve artificial *in situ* light reduction. Coarse mesh (1.91 x 1.91 cm) reduced irradiance to 14% of surface irradiance (SI) while fine mesh (0.64 x 0.64 cm) reduced irradiance to 5% SI. Cages without a top screen were placed on the seagrass bed as controls. Three replicate cages for each treatment were deployed in a random manner in the seagrass bed. The shading mesh was replaced with cleaned mesh every one or two weeks to minimize the effects of fouling on light transmissivity. The perimeter of each cage was cut to a sediment depth of about 30 cm to physiologically isolate plants located within and outside of the cages. Shading was initiated in late April 1993 and terminated in August 1994. The experiment lasted a total of 490 days. No data exist for fine mesh cages (5% SI) after November 1993, since all plants within these cages died by that date.

Biological Measurements Quarterly measurements of plant density, biomass, leaf chlorophyll content, blade width and leaf elongation rates were made in the experimental cages.

RESULTS

Underwater Irradiance The annual quantum flux at the surface was 12983 mol m^{-2} yr^{-1}, and ranged from an average of 55.7 in July to 18.4 mol m^{-2} day^{-1} in December 1993 (Fig. 5-1). The annual quantum flux at the seagrass canopy was 5207 mol m^{-2} yr^{-1}, which corresponded to 46% SI. Two light manipulation treatments using coarse and fine mesh significantly reduced ($P < 0.001$) underwater irradiance to 1628 (14% SI) and 864 mol m^{-2} yr^{-1} (5% SI) respectively. In control cages, underwater photon flux density (PFD) ranged from 9 to 22 mol m^{-2} day^{-1} (average 14.3 mol m^{-2} day^{-1}). Average PFD in the cages shaded with coarse and fine mesh was 4.5 and 2.4 mol m^{-2} d^{-1} respectively (Table 5-1). Unlike surface measurements of PAR, underwater PFD did not exhibit a seasonal sigmoidal curve.

Pore water Ammonium and Sulfide Sediment pore water ammonium concentrations were measured three times (September 1993 and April and July 1994) during the course of this study. Pore water ammonium concentrations in 14% and 5% SI cages were significantly ($P < 0.001$) higher than controls (46% SI). Pore water ammonium concentrations for control cages ranged from 62 µM NH_4^+ in April 1994 to 101 µM NH_4^+ in July 1994. The concentrations in 14% SI treatment cages ranged from 141 µM NH_4^+ in April 1994 to 179 µM NH_4^+ in July 1994 (Fig. 5-2). There was no significant difference in pore water ammonium concentrations between sites receiving 14% SI and 5% SI in September 1993, shortly before all plants at 5% SI died.

Pore water sulfide concentrations of the control and 14% SI cages in August 1994 were 107 µM and 179 µM sulfide, respectively. The concentration of sulfides in the shaded cages was significantly ($P = 0.01$) higher than in the controls.

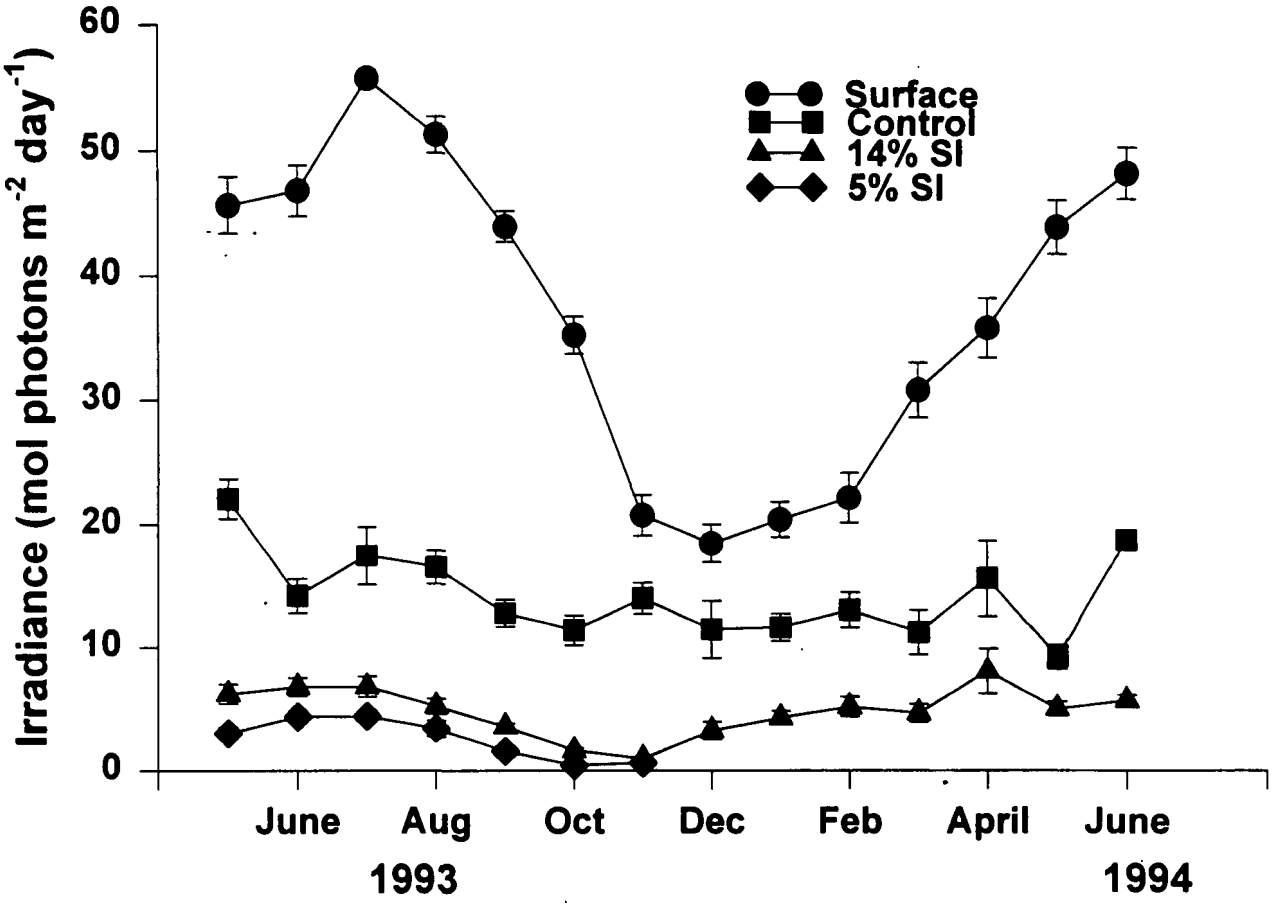


Fig. 5-1. Average daily photo flux density (PFD) collected underwater (control, 14% SI and 5% SI treatment cages) and at the surface (The University of Texas Marine Science Institute in Port Aransas). Data collection at the 5% SI treatment was terminated in November 1993 following the death of all plants in these cages.

Shoot Density and Blade Width Shoot densities in control cages (46% SI) ranged from 457 to 785 m^{-2}. Shoot densities in 14% and 5% SI cages were significantly ($\underline{P}$ <0.001) lower than controls throughout the experiment (Fig. 5-3). In August 1993, after 116 days shading, shoot densities in the various treatments were 785 m^{-2} (control), 296 m^{-2} (14% SI), and 168 m^{-2} (5% SI). All plants exposed to 5% SI died after 200 days of shading treatment and over 99% of plants receiving 14% SI died by the end of the experiment (490 days).

Blade widths in *Thalassia testudinum* decreased significantly ($\underline{P}$ <0.001) as a result of light reduction, with blade width decreasing more rapidly in plants at 5% SI than those at 14% SI (Fig. 5-4). After only 36 days of shading (May 1993), blade widths of plants receiving 5% SI had already decreased significantly ($\underline{P}$ <0.001) to 6.0 mm compared to plants in the control and at 14% SI. In August, after 128 days of shading, blade widths of plants at 5% SI averaged 4.7 mm compared to plants at 14% SI, which were 6.6 mm in May 1993, but decreased to 4.8 mm in April and July 1994. Blade widths of control plants ranged from 6.4 to 7.0 mm during the entire period.

Chlorophyll Content Total chlorophyll (chl $\underline{a}$ + chl $\underline{b}$) from control plant leaves ranged from 5.0 mg chl g^{-1} dry wt in July 1993 to 6.7 mg chl g^{-1} dry wt in July 1994 (Fig. 5-5). Total blade chlorophyll and chl $\underline{b}$ content increased significantly ($\underline{P}$=0.019 and $\underline{P}$ <0.001 respectively) with decreased levels of PAR. Chl $\underline{a}$ levels also

	Control	Light Manipulation	
	(*in situ* ambient)	Coarse mesh	Fine mesh
Average PFD (mol photons m^{-2} day^{-1})	14.27	4.46	2.37
% ISA	100	31.4	16.1
% SI	46.4	14.3	5.4
H_{sat} (h)	8.5	3.3	0.9
Total irradiance (mol m^{-2} yr^{-1})	5207	1628	864

Table 5-1 Daily average photon flux density (PFD), % of *in situ* ambient (%ISA), % of surface irradiance (%% SI) and the daily period of light saturated photosynthesis (H_{sat}) in control and light manipulation cages. H_{sat} values based on a saturation irradiance of 140 μmol m^{-2} s^{-1} for *Thalassia testudinum* (Dunton, unpub. data).

showed an increasing trend with light reduction, but it was not statistically significant (P=0.11). Total blade chlorophyll concentrations in 5% SI plants ranged from 5.4 mg chl g^{-1} dry wt in September 1993 to 6.5 mg chl g^{-1} dry wt in July 1993, while chlorophyll concentrations were lowest (6.0 mg chl g^{-1} dry wt) in July 1993 and highest (8.3 mg chl g^{-1} dry wt) in July 1994 for plants at 14% SI.

The chl a : b ratios of blades from control cages ranged from 2.7 in September 1993 to 3.4 in July 1994 (Table 5-2). Chl a : b ratios of blade tissue decreased significantly (P<0.001) as a result of the two light reduction treatments. The ratios were highest in plants receiving 46% SI and lowest in the plants receiving 5% SI. Chl a: b ratios of 14% SI plants was highest (2.7) in April 1994 and lowest (2.1) in July 1994, while plants at 5% SI showed chl a : b ratios of 2.4 in July 1993 and 2.5 in September 1993.

Leaf Production Rates Leaf production rates were highest during summer and lowest during the cooler months (Fig. 5-6), ranging from 1.5 mg $shoot^{-1}$ d^{-1} (0.7 g m^{-2} d^{-1}) in April 1994 to 5.0 mg $shoot^{-1}$ d^{-1} (2.4 g m^{-2} d^{-1}) in July 1994 in control plants. Leaf production rate per shoot (mg $shoot^{-1}$ d^{-1}) and areal leaf production rate (g m^{-2} d^{-1}) decreased significantly (P <0.001) with shading. In May and August 1993, leaf productivities of plants receiving 14% SI were 3.8 and 2.5 mg $shoot^{-1}$ d^{-1}, compared to plants at 5% SI, which were 1.9 and 1.2 mg $shoot^{-1}$ d^{-1}. Areal leaf productivity at 5 and 14% SI dropped to nearly zero after about one year of shading as a result of extremely low shoot densities.

Biomass Biomass decreased significantly (P <0.001) with light reduction. In August 1993, 116 days after shading, the biomass in cages at 14% SI decreased to less than half that of controls and was less than a third of control biomass within the 5% SI treatments (Table 5-3). All plants receiving 5% SI died by November 1993, after 200 days of reduced PAR. The biomass of the plants receiving 14% SI decreased to 20% of control biomass by April 1994 (after 345 days of shading), and to 1.4% of control biomass by July 1994 (after 457 days of shading).

Relative to controls, leaf biomass decreased more rapidly than biomass of below-ground tissues under light reduction. In August 1993, after 116 days of shading, the leaf biomass of plants at 5% SI decreased 95%

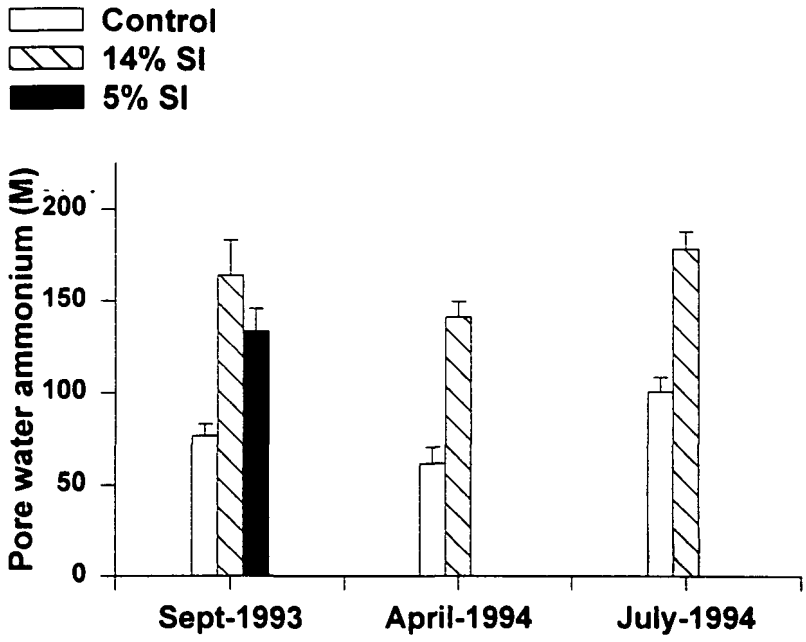


Fig. 5-2. Pore water ammonium concentration in sediments of control, 14% SI and 5% SI treatment cages. Values are means ± SE (n=3).

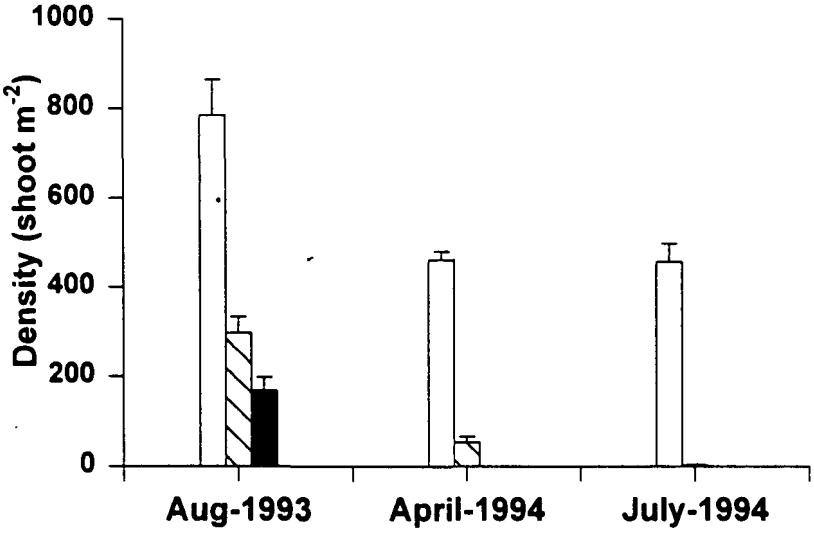


Fig. 5-3. Shoot densities in control, 14% SI and 5% SI treatment cages. Values are means ± SE (n=3).

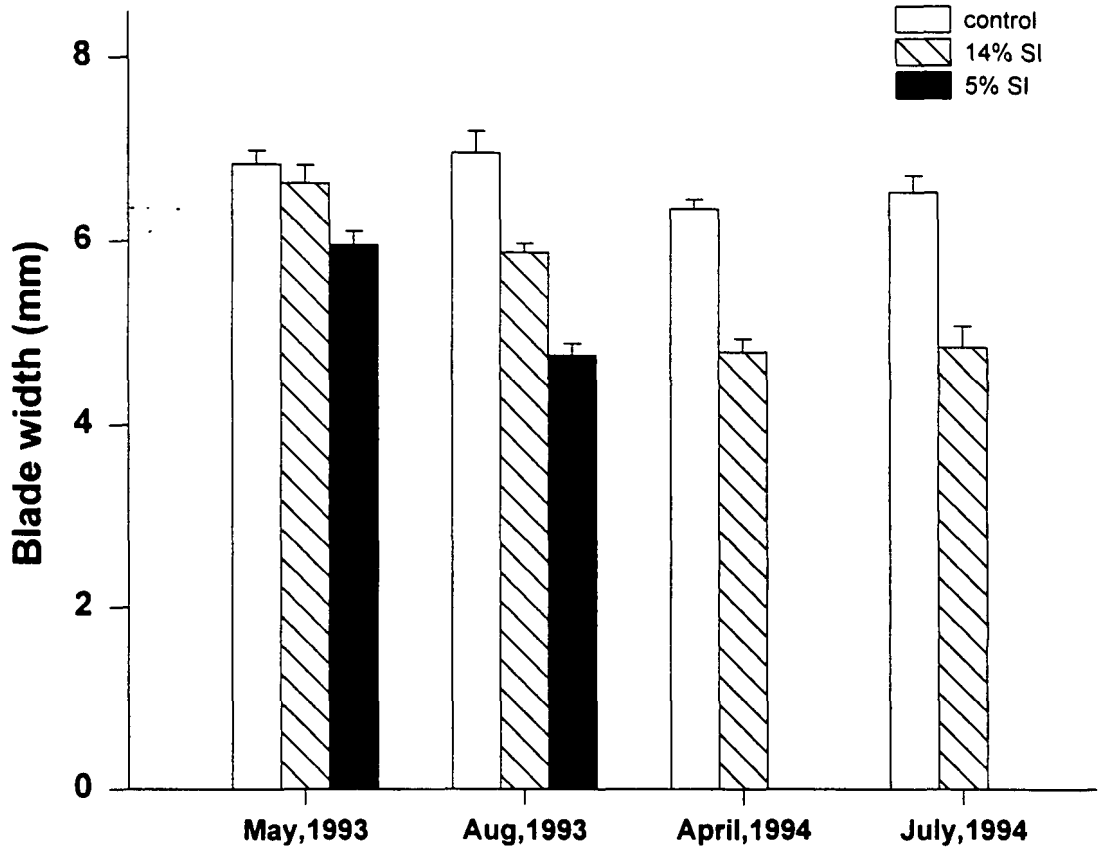


Fig. 5-4 Blade widths of *Thalassia testudinum* from control, 14% SI and 5% SI treatment cages. Values are means ± SE (n=3).

compared to a corresponding drop of 50% in below-ground biomass. After loss of leaf material, root biomass decreased rapidly. In April 1994, after 345 days of shading, root biomass decreased 90% at 14% SI, while short stem and rhizomes maintained 20-30% of their biomass relative to controls. Although rhizome material was the most durable plant part, biomass of this component dropped 98% by the end of the experiment.
In control plants, below/above-ground ratios changed significantly with season (P=0.0015). The ratio was lowest (1.3) in August and highest (5.8) in April (Table 5-4). Percentage of leaf (above-ground) biomass as a function of total biomass was highest in August 1993, while that of rhizome was highest in April 1994. The percentages of short stem and root biomass were fairly constant. Leaf biomass accounted for 45% of total biomass in August, while accounting for only 17% in April. Rhizome biomass was 20-40% of total biomass in July and August and about 50% of total biomass in April (Fig. 5.7).

Below/above-ground ratios significantly (P <0.001) increased with light reduction (Table 5-4). In August 1993 the ratio of plants receiving 46% SI was 1.3 while those of plants receiving 14% and 5% SI were 3.0 and 14.7, respectively. By July 1994 the below/above-ground ratio of control plants was 2.1 compared to 14.0 for plants at 14% SI; this difference was reflected by rhizome tissues, which constituted nearly 70% of the total plant biomass in plants at 14% SI compared to 40% for control plants (Fig. 5-7).

Carbohydrate Carbon Soluble carbohydrate carbon content of plants at 46% SI was highest in rhizomes (130-136 mg C g^{-1} dry wt) and in short stem (102-152 mg C g^{-1} dry wt), and relatively low in leaf (50-66 mg C g^{-1} dry wt) and in root tissue (57-74 mg C g^{-1} dry wt) (Fig. 5-8). Shading treatments significantly (P <0.001) lowered the soluble carbohydrate carbon content of leaf, rhizomes and short stem. However, the content of root tissue did not change significantly (P=0.53) with light reduction. Soluble carbohydrate levels in rhizomes

and short stem decreased more rapidly with reduced light than that of leaf material. In both shading treatments rhizome carbohydrate carbon content was 50% lower and leaf carbon content was about 15% lower than controls. In April 1994, total carbohydrate carbon content in control plants ranged from 107 mg C g^{-1} dry wt in leaf to 158 mg C g^{-1} dry wt in rhizome tissues (Table 5-5). Total carbohydrate carbon content decreased to 91 mg C g^{-1} dry wt in leaf and 127 mg C g^{-1} dry wt in rhizome tissues with light reduction. Structural carbohydrate carbon content was estimated by subtraction of soluble carbohydrate carbon content from total carbohydrate carbon content. In leaf tissues of control plants, about 50% of total carbohydrates was attributed to structural carbohydrate, while only 20% in rhizome tissues was structural. Structural carbohydrate carbon content in plant tissues did not decrease with light reduction.

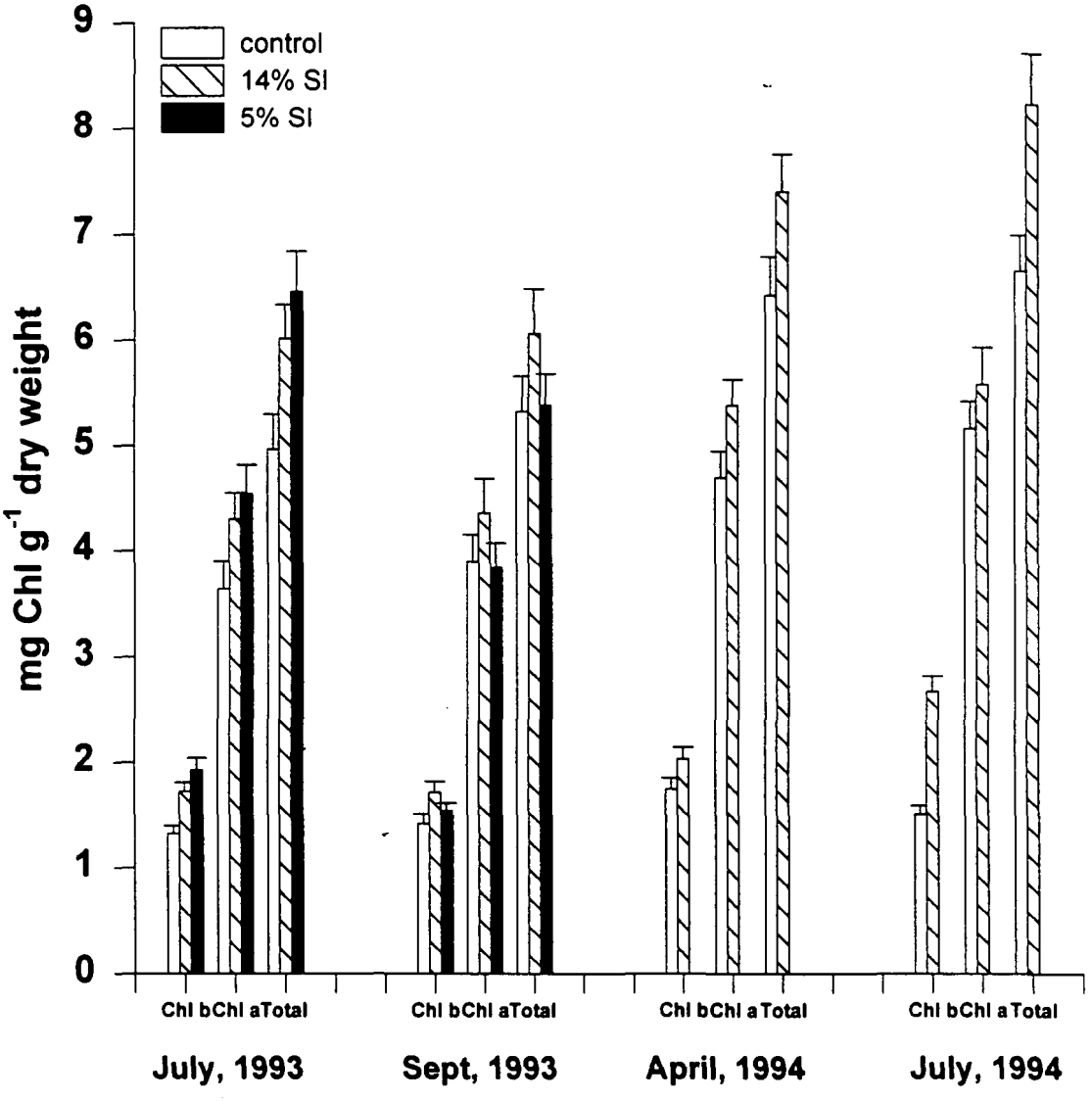


Fig. 5-5. Chlorophyll a, chlorophyll b and total (chl a+b) concentrations of *Thalassia testudinum* leaves from control, 14% SI and 5% SI treatment cages. Values are means ± SE (n=3).

Chlorophyll a:b ratio			
Sampling Date	Control	14% SI	5% SI
July 1993	2.74 ± 0.09	2.51 ± 0.08	2.37 ± 0.08
Sept. 1993	2.72 ± 0.05	2.52 ± 0.06	2.48 ± 0.06
April 1994	2.73 ± 0.07	2.67 ± 0.05	nd
July 1994	3.44 ± 0.10	2.10 ± 0.07	

Table 5-2. Chlorophyll a:b ratio of *Thalassia testudinum* leaves from control, 14% SI and 5% SI treatment cages at four different sampling times. Values are means ± SE (n=3). nd: no data

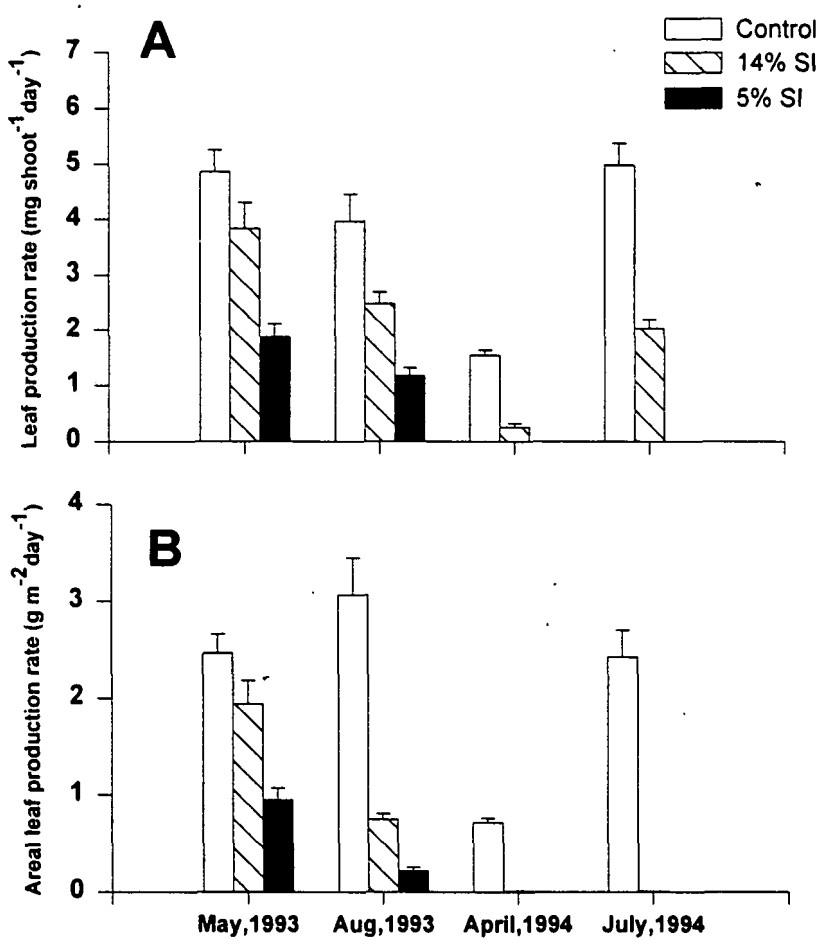


Fig. 5-6. Daily leaf production on a shoot (A) and areal (B) basis in control and treatment cages. Values are means ± SE (n=3).

Sampling Date (Days shaded)	Biomass (g dry wt m^{-2})			
	May 1993 (0)	August 1993 (116)	April 1994 (345)	July 1994 (457)
Total				
Control	577.0 ± 79.3	971.2 ± 111.2	367.5 ± 34.4	561.5 ± 85.5
14% SI	nd	421.4 ± 40.4	73.8 ± 19.0	21.1 ± 11.8
5% SI	nd	307.9 ± 56.0	nd	nd
Leaf				
Control	240.6 ± 28.0	445.3 ± 68.2	63.4 ± 10.5	181.2 ± 25.6
14% SI	nd	122.1 ± 24.4	7.8 ± 2.5	0.6 ± 0.4
5% SI	nd	30.1 ± 8.0	nd	nd
Rhizome				
Control	182.6 ± 36.7	200.7 ± 38.6	185.6 ± 12.1	216.8 ± 29.4
14% SI	nd	114.6 ± 15.1	36.3 ± 9.6	14.3 ± 10.1
5% SI	nd	129.6 ± 11.5	nd	nd
Short shoot				
Control	98.2 ± 17.8	195.7 ± 25.9	87.4 ± 17.9	123.3 ± 32.3
14% SI	nd	110.8 ± 20.4	25.9 ± 7.8	6.0 ± 6.0
5% SI	nd	103.6 ± 32.1	nd	nd
Root				
Control	55.6 ± 9.7	129.6 ± 11.0	31.3 ± 5.1	40.2 ± 5.1
14% SI	nd	73.9 ± 8.5	3.7 ± 1.1	0.2 ± 0.2
5% SI	nd	44.6 ± 14.3	nd	nd

Table 5-3. Biomass changes in total and individual plant parts as a result of light manipulation in May (initial sampling date) and August 1993 and April and July 1994. No plants survived in the 5% treatment cages after November 1993. Values are means ± SE (n=3). nd: no data.

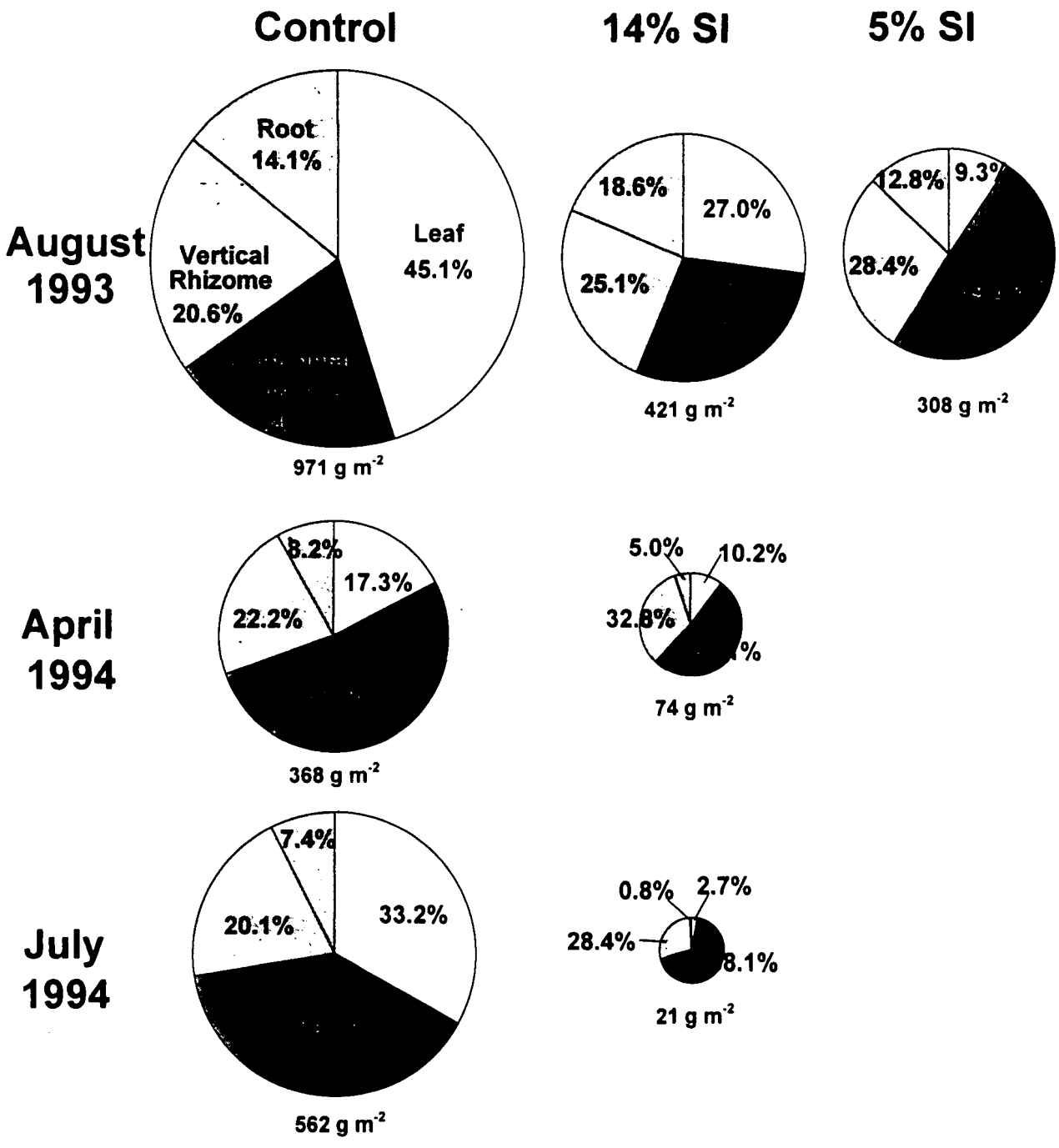


Fig. 5-7. Changes in biomass partitioning of *Thalassia testudinum* into different plant parts (leaf, short stem, rhizome and roots) as a result of light manipulation between August 1993 and July 1994. Circle area corresponds with total plant biomass listed for each site/date combination.

Sampling Date		Below/above-ground ratio	
	Control	14% SI	5% SI
August 1993	1.3 ± 0.2	3.0 ± 0.6	14.7 ± 6.0
April 1994	5.8 ± 0.9	12.4 ± 2.9	nd
July 1994	2.1 ± 0.2	14.0 ± 3.9	nd

Table 5-4. Below-to above-ground ratios of *Thalassia testudinum* at 46% SI (control), 14% SI and 5% SI in August 1993 and April and July 1994. Values are means ± SE (n=3). nd: no data.

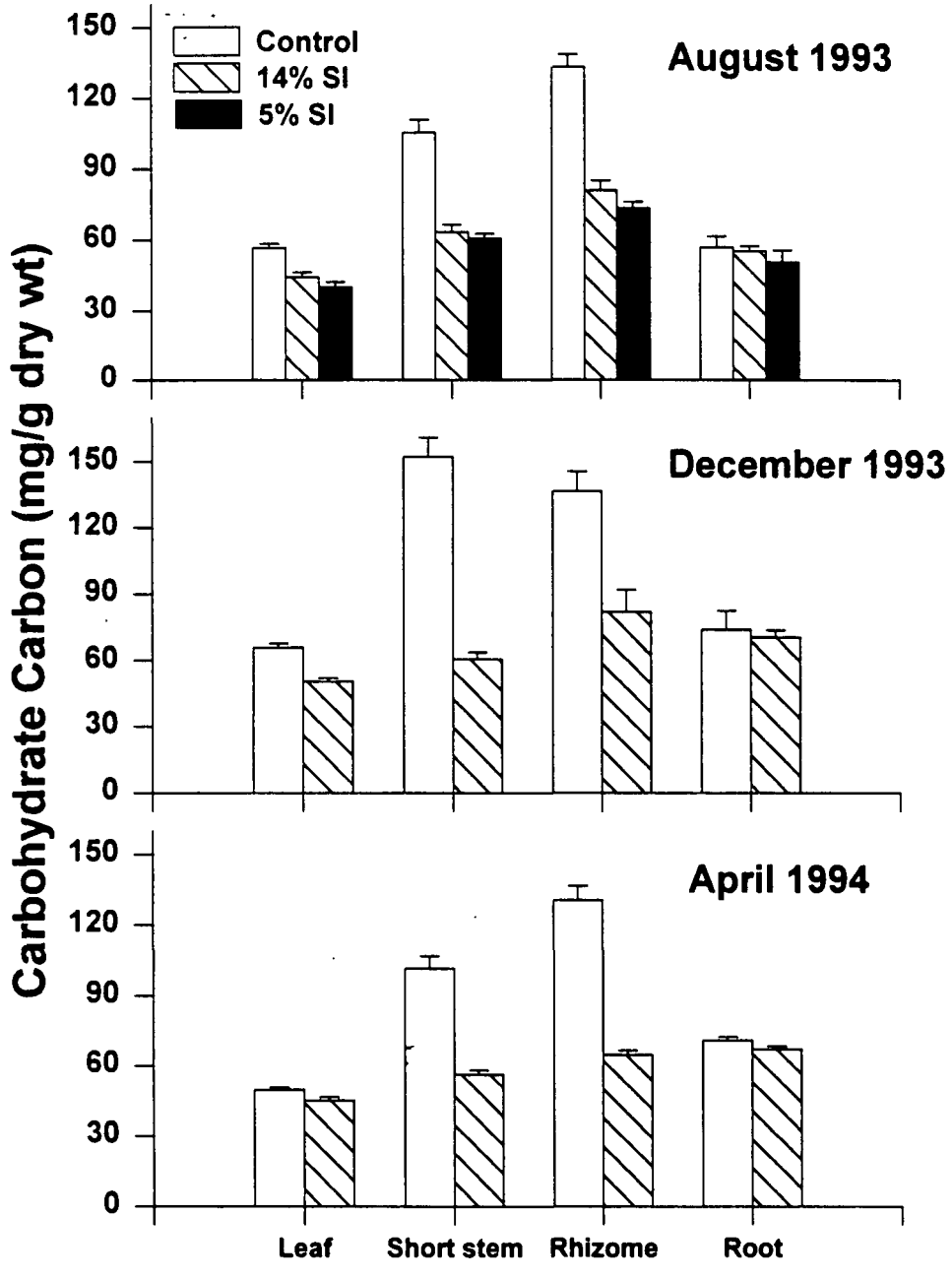


Fig. 5-8. Carbohydrate carbon concentration in different plant tissues of *Thalassia testudinum* from control and light treatment cages in August and December 1993 and April 1994. Values are means ± SE (n=3).

Carbohydrate carbon	Control cage				14% SI			
(mg C gdw^{-1})	Leaf	Rhizome	Short stem	Root	Leaf	Rhizome	Short stem	Root
Total	107.0 ± 4.8	157.5 ± 4.4	115.2 ± 4.4	107.4 ± 2.0	91.0 ± 4.5	127.1 ± 3.2	90.4 ± 3.3	117.1 ± 2.1
Soluble	49.7 (46) ± 1.1	130.5 (83) ± 6.1	101.6 (88) ± 5.4	70.9 (66) ±1.4	45.0 (49) ± 1.6	64.7 (51) ± 1.9	56.2 (62) ± 1.8	67.1 (57) ± 1.3
Structural	57.4 (54) ± 4.2	27.0 (17) ± 10.6	13.6 (12) ± 4.8	36.5 (34) ± 3.5	46.0 (51) ± 3.4	62.4 (49) ± 3.0	34.2 (38) ± 1.2	50.0 (43) ± 2.1

Table 5-5. Total, soluble and structural carbohydrate carbon content of different plant tissues of *Thalassia testudinum* from control and 14% SI cages in April 1994. Values are means ± SE (n=3). Numbers in parentheses represent the percent soluble or structural carbohydrate carbon of total.

DISCUSSION

In situ* light requirements of *Thalassia testudinum Light reduction resulted in decreases in shoot density and biomass in *Thalassia testudinum*. Plants in the control cages (46% SI) remained healthy throughout the experiment; in contrast, all plants at 5% SI died within 7 months, and most shoots at 14% SI died after 16 months. Czerny & Dunton (1995) also demonstrated that *Thalassia testudinum* did not tolerate a light reduction equivalent to 14% SI. This finding is consistent with the minimum light requirements (15-25% SI) reported by Dennison et al. (1993) for *Thalassia testudinum* from Florida and the Caribbean. Further long-term measurements of *in situ* PAR in *Thalassia testudinum* beds at variety of depths is needed to establish the minimum light requirements for Texas plants as has been done for *Halodule wrightii* (Dunton, 1994).

Thalassia testudinum showed various morphological and physiological adaptations in response to changes in underwater light availability. Seagrasses can respond to light reduction by increasing chlorophyll content and decreasing their chl a : b ratio (Wiginton & McMillan, 1979; Dennison & Alberte, 1982, 1985; Abal et al., 1994). We found agreement with these trends as shown by increases in chlorophyll concentrations and decreases in chl a : b ratios in response to light reduction, although some of these changes were not statistically significant. Wiginton & McMillan (1979) reported that chl a : b ratios were correlated with depth distribution of seagrasses; additionally, they suggested that the chl a : b ratios controlled distributional differences among species. Seagrass occurring in deep areas had low chl a : b ratios, but seagrass occurring at shallow depths had a higher ratio. They suggested that differences in chl a : b ratios were a response to reduced PFD at depth, and not to changes in light quality. However, measurements of underwater spectral irradiance (Weidemann & Bannister, 1986; McPherson & Miller, 1987) indicated that the wavelengths absorbed by chl a decreased more rapidly than the wavelengths absorbed by chl b with increasing water depth. Thus, although plants receiving less light may increase their total chlorophyll concentration to increase light absorption efficiency, rapid increases in chl b relative to chl a would allow more efficient use of the more abundant wavelengths at depth.

Seagrass blade width has been correlated with environmental factors that are ultimately related to underwater light regimes as noted by several investigators (McMillan, 1978; McMillan & Phillips, 1979; Phillips & Lewis, 1983). For example, McMillan (1978) noted that *Thalassia* populations from turbid bays were characterized by having narrower leaves compared to plants in clear water. Phillips & Lewis (1983) found that *Thalassia* blade width decreased with increasing depth, and suggested that light attenuation was the causal factor. Our results indicate that decreased light availability has a significant and almost immediate effect on blade width, which decreased about 2 mm (to 4.7 mm) as a function of light reduction and shading duration. Since attainment of the minimum 4.7 mm width was subsequently followed by plant death, decreases in blade width may be a convenient indicator of light stress in *Thalassia testudinum*.

Changes in biomass and carbon budget Many studies suggest that whole plant carbon balance is a major factor determining the growth and distribution of seagrasses (Dennison & Alberte, 1982, 1985; Marsh et al., 1986; Zimmerman et al., 1989; Fourqurean & Zieman, 1991; Zimmerman et al., 1991). Carbon balance has often been estimated from rates of respiration and photosynthesis vs. irradiance curves constructed for above-ground tissues only (Dennison & Alberte, 1985; Marsh et al., 1986; Zimmerman et al., 1991), but there are several other factors that must be considered. These factors include a knowledge of carbon and biomass partitioning into different plant parts, carbon metabolism of below-ground tissues, storage of photosynthate and root anoxia.

Leaf biomass from control cages accounted for almost 50% of total biomass of *Thalassia testudinum* during the warm growing season, and decreased more rapidly than biomass of below-ground tissues as a result of reduced light. Percent leaf biomass as a function of total biomass decreased from 45% to 9.3% in plants at 5% SI during the first four months. Decreased leaf biomass in the shaded cages is probably a product of both defoliation and decreased leaf growth. Defoliation is a normal response of terrestrial and submerged plants to reduced light levels (Addicott & Lyon, 1973; Backman & Barilotti, 1976; Neverauskas, 1988), but defoliation during the active growing season may seriously impact seagrass survival through decreases in the production and transport of oxygen to below-ground tissues.

Root biomass decreased more rapidly than rhizome biomass with light reduction. Plants receiving 14% SI for 345 days lost about 90% of their root biomass, while rhizomes still maintained 20~30% of their biomass relative to controls. Results from a litter bag decomposition experiment indicate that *Thalassia* rhizome is more resistant to decay than root tissues (Kenworthy & Thayer, 1984), which is in agreement with our findings. The increase in the decomposition of below-ground material under low light conditions may also contribute to increases in pore water ammonium and sulfide levels.

The below-ground tissues of seagrasses generally exist in an anoxic environment (Penhale & Wetzel, 1983). In addition to lack of oxygen for aerobic respiration of below-ground tissues, sulfide is produced in anaerobic sediments by bacteria using sulfate as a terminal electron acceptor (Sorensen et al., 1979). Sulfide inhibits respiration, oxygen release and nutrient uptake by plant roots (Bagarinao, 1992). In Florida Bay, pore water sulfide concentrations were considerably higher in die-off areas than in healthy *Thalassia* beds (Carlson et al., 1994) suggesting that sulfide toxicity may play a role in the loss of seagrass. Photosynthetically produced oxygen is secreted into sediment through roots (Smith et al., 1984), supporting aerobic metabolism and creating an oxidized zone around the roots where pore water sulfide and ammonium oxidation can occur. In this study, the concentration of pore water ammonium and sulfide in shaded cages were significantly higher than that from control cages. This suggests that below-ground tissues in shaded cages were exposed to anoxic conditions more frequently than controls. *Thalassia testudinum* is more vulnerable to anoxia than other seagrass species because of the relatively high ratio of below-ground biomass to above-ground biomass and its deep rooted growth habit.

Soluble carbohydrate carbon content was highest in rhizome tissues and likely serves as an energy reserve for plant sustenance during the winter period (Dawes & Lawrence, 1980; Durako & Moffler, 1985). In this study levels of soluble carbohydrates decreased significantly in all plant tissues (except roots) with reduced light; however, different plant parts showed distinctive decreasing patterns. Soluble carbohydrate levels in rhizomes and short stems decreased to half that of control plants with light reduction, while levels decreased slightly in blades but remained constant in roots. However, structural carbohydrate levels in plant tissues did not decrease with light reduction. Stored carbohydrate in rhizome tissues can be used to meet the respiratory demands of the plant and can contribute to new growth in above-ground tissues during periods of low photosynthetic production (Dawes & Lawrence, 1979, 1980; Pirc, 1985; Dawes & Guiry, 1992). In addition, when below-ground tissues respire anaerobically, carbon demand increases to meet the metabolic requirements of plants, further decreasing carbohydrate reserves. We found that the demands on stored carbon reserves depleted carbohydrates in rhizome tissues to the levels equivalent to that in the leaves and roots, and consequently the plants were not capable of providing reduced carbon compounds to meet their daily metabolic energy requirements.

In summary, *in situ* light reduction resulted in a rapid decrease in leaf biomass in *Thalassia testudinum* through

defoliation and low leaf elongation rates. The drop in leaf biomass enhanced anoxia in sediments through decreases in photosynthetic oxygen production and transport to below-ground tissues, ultimately raising the concentration of toxic sulfides and promoting root anaerobic fermentation. Utilization and rapid depletion of stored carbohydrate reserves in rhizome tissues, combined with low productivity and high concentrations of sediment sulfides, resulted in plant loss at light levels equivalent to 5 and 14% SI (864 and 1628 mol m^{-2} yr^{-1}, respectively). Our results also indicate that the effects of light reduction in *Thalassia testudinum* are reflected in a variety of parameters which are conveniently monitored, including shoot density, blade width, leaf growth, chl a : b ratio and chlorophyll content. These parameters are potentially valuable indicators of seagrass health based on their sensitivity and relatively rapid response to changes in underwater irradiance, and consequently can be important tools in the management of submerged aquatic vegetation (Neckles, 1994).

VI. SEDIMENT SULFIDE AND PHYSIOLOGICAL RESPONSES OF *THALASSIA TESTUDINUM* TO SHADING.

Paul R. Carlson, Jr.,

INTRODUCTION

Drastic declines in the distribution and abundance of estuarine seagrass and submerged aquatic vegetation (SAV) communities have occurred in many estuaries throughout the Gulf of Mexico as the result of concurrent declines in water quality. Benthic aquatic plants are particularly sensitive to decreased light availability due to phytoplankton blooms, sediment resuspension, and nutrient-stimulated epiphytes.

This report describes our contribution to a collaborative research project funded by the U. S. Environmental Protection Agency and coordinated by Dr. J. C. Zieman of the University of Virginia. The overall objective of this project was to determine the effects of light attenuation on the survival and growth of turtle grass (*Thalassia testudinum*). We focused on the physiological responses of *Thalassia* to light attenuation and the potential role of sediment sulfide as a synergistic stressor which might amplify the effects of light attenuation on *Thalassia* .

METHODS

Sulfide- Pore water sulfide samples were collected by two methods. From March 1993 until November 1993 pore water samples were collected monthly using suction lysimeters, or "sippers." From December 1993 until September 1994, pore water sulfide concentrations were determined quarterly on sediment cores collected by hand coring from each enclosure. Sulfide concentrations from sipper samples and sediment cores were determined using a sulfide ion-specific electrode (Orion Model 95-01).

Physiological Parameters- Rhizome samples were collected quarterly from each enclosure. Rhizome segments were transferred to scintillation vials, frozen with liquid nitrogen, and transported to FMRI on dry ice. Prior to analysis, samples were stored at -70 deg. C. To avoid "oversampling" within enclosures, we limited quarterly collection of belowground tissue to one core per enclosure. As a result, we analyzed four mature rhizome segments per enclosure, instead of two mature rhizome segments and two rhizome apices as we originally planned. In fall 1993, we began collecting Thalassia rhizomes outside enclosures at the Rabbit Key Basin (RKB) and St. Joseph's Bay (SJB) sites to serve as outside controls.

Four analyses were performed on each rhizome segment. Alcohol dehydrogenase (ADH) analyses were performed by the procedure of Bergmeyer (1974). ADH activity was calculated two ways: 1. raw activity divided by tissue fresh weight and 2. activity normalized to tissue protein concentration. Protein was determined by the Coomassie Blue procedure as modified by Appenroth an Augsten (1987). Extractable sugars and starch were determined by a sequential extraction procedure (Zimmermann et al., 1989) which uses 80% ethanol to extract sugars and 1N NaOH to extract starch from rhizome tissue. For purposes of discussion, the sum of extractrable sugars and extractable starch is described below as total carbohydrate.

Statistical analyses (tests of normality, analyses of variance, and multiple range tests) were conducted using SAS Release 6.03 (SAS Institute, 1988). To facilitate comparison among sites, separate analyses of variance (ANOVA) were performed for fall 1993, spring 1994, and summer 1994 collections. Spring 1993 (time-zero)

comparisons among sites were made using initial collections from each site: March 1993 at St. Joseph's Bay, April 1993 at Rabbit Key Basin and Sunset Cove; and June 1993 at Corpus Christi Bay.

RESULTS

Spring 1993- Significant differences among sites were observed for all physiological parameters in the time-zero samples (Table 6-2). Corpus Christi Bay samples had protein, sugar, starch, and total carbohydrate concentrations and ADH activities which were consistently lower than those of other sites. For most parameters, values were highest at Rabbit Key Basin and slightly lower at St. Joseph's Bay; for some parameters the difference was statistically significant, for others it was not. Sunset Cove values for most parameters were intermediate between those for St. Joseph's Bay and those for Corpus Christi Bay. The pattern of protein concentrations among sites differed from the pattern for other parameters: values were highest at St. Joseph's Bay, lower at Sunset Cove and Rabbit Key Basin, and lowest at Corpus Christi Bay.

Fall 1993- When data from all treatments were pooled for each site, significant differences among sites were noted for rhizome ADH activity, protein, sugar, starch, and total carbohydrate concentrations (Table 6-1). ADH activity ranged from 2.68 umol/min/gFW at St. Joseph's Bay to 1.117 umol/min/gFW at Corpus Christi Bay (Table 6-2). Normalized ADH values showed a similar trend; values were highest at St. Joseph's Bay, slightly lower at Rabbit Key Basin and Sunset Cove, and significantly lower at Corpus Christi Bay. Protein concentrations were highest at St. Joseph's Bay and Corpus Christi Bay, lower at Rabbit Key Basin, and lowest at Sunset Cove.

Total carbohydrate was much higher at Rabbit Key (71 mg/gFW) than at other sites (Table 6-2). Values at Corpus Christi Bay and St. Joseph's Bay were intermediate, while Sunset Cove values (21 mg/gFW) were lowest. Similar patterns were seen in extractable sugar and starch concentrations.

Significant treatment effects were seen for all physiological parameters when data from all sites sampled in fall 1993 were pooled (Table 6-1). ADH activities (raw and normalized) were significantly higher in outside control and control treatments than in coarse or fine mesh treatments (Table 6-3). ADH activities in fine and coarse mesh treatments were not significantly different from one another.

Total carbohydrate concentrations in outside controls (115 mg/gFW) were significantly higher than those of control enclosures (69 mg/gFW). Total carbohydrate concentrations of both coarse and fine mesh treatments were not significantly different from one another but were significantly lower than those of control enclosures. Similar patterns were seen in extractable sugar and starch concentrations.

ADH activity exhibited a strong treatment effect at three of the four sites sampled in fall 1993. ADH activity of control enclosures was significantly higher than that of coarse and fine treatment enclosures at the Corpus Christi Bay (CCB) and Sunset Cove (SUN) sites (Fig. 6-1). At the Rabbit Key Basin site (RKB), ADH activity of outside controls and control enclosures was significantly higher than that of the fine mesh enclosures. While the ADH activity of RKB coarse mesh enclosures was lower than that of controls and higher than that of fine mesh enclosures, the differences were not statistically significant. Differences among treatments at the St. Joseph's Bay (SJB) site were not significantly different. Patterns for normalized ADH activities were similar to those for raw ADH activity. However, fewer significant differences among treatments were noted for normalized ADH activities.

Although protein concentrations exhibited significant differences among treatments, the pattern is difficult to interpret. Protein in the coarse mesh treatment is significantly lower than that of both control and outside control treatments, but concentrations in the fine mesh treatment are not significantly different from those of any other treatment (Table 6-3). Examining protein concentrations site by site (Fig. 6-2), values in the coarse mesh treatment appear to be lower (but not significantly lower) than those of other treatments at each site.

Carbohydrate parameters (sugar, starch, and total carbohydrate) exhibited marked treatment effects in fall 1993. At all sites, total carbohydrate in the control treatment was higher than values in either (coarse or fine

mesh) shaded treatment (Fig. 6-2). However, coarse and fine mesh treatments values were not significantly different at any site. At St. Joseph's Bay and Rabbit Key Basin (the only two sites where outside control samples were collected), total carbohydrate was significantly greater in outside controls than in control enclosures.

Extractable sugar concentrations (Fig. 6-3) exhibited a pattern similar to total carbohydrate. For all sites except St. Joseph's Bay, sugar concentrations in control treatments were significantly higher than values in either coarse or fine mesh treatments. At all four sites, sugar concentrations in the two shaded treatments were not significantly different from one another. As noted for total carbohydrates, sugar concentrations in outside control samples at Rabbit Key Basin and St. Joseph's Bay sites were significantly higher than values in control enclosures.

Fewer significant differences among treatments were noted for starch concentrations than for total carbohydrate and extractable sugars. Outside control starch values were higher than control enclosure values, and shaded enclosure values were uniformly low, but starch concentrations from control enclosures were not significantly higher than those of the shaded enclosures for three of four sites.

Spring 1994- Protein, sugar, and total carbohydrate concentrations, as well as ADH activities (raw and normalized), varied significantly among sites in spring 1994 (Tables 6-1, 6-2). Values for most parameters at the Corpus Christi Bay site were significantly lower than those of St. Joseph's Bay or Rabbit Key Basin. However, protein concentrations at both St. Joseph's Bay and Corpus Christi were significantly lower than at Rabbit Key Basin.

Significant treatment effects were noted for ADH activities (raw and normalized), extractable sugar, and total carbohydrate. Protein and starch concentrations, however, did not vary significantly among treatments (Table 6-3).

Differences in patterns among treatments in fall 1993 and spring 1994 result from the removal of shade screens from the fine mesh enclosures after fall 1993 samples were collected. Six months later, levels of most parameters in the open fine mesh enclosures were not significantly different from values in control enclosures. However, sugar, total carbohydrate, and ADH activity were significantly lower in coarse mesh cages than in control enclosures. Although sugar, starch, total carbohydrate, and ADH activity were higher in the outside controls than in the control enclosures, the difference was not significant. Protein and starch concentrations did not vary significantly among treatments at any site in spring 1994.

At the Corpus Christi site, ADH activity of the control treatment was significantly higher than that of the shaded, coarse-mesh enclosures. At Rabbit Key Basin, ADH activity was significantly greater in control enclosures than in coarse or fine mesh enclosures; outside control values were variable and generally lower than control enclosures. At St. Joseph's Bay, normalized ADH concentrations of fine mesh (open) enclosures was not significantly lower than values for outside controls. Differences between ADH values in control enclosures and coarse mesh enclosures were not significant at St. Joseph's Bay.

Although starch concentrations did not vary significantly among treatments at any site in spring 1993, the general pattern of sugar, starch, and total carbohydrate concentrations shows recovery of fine mesh enclosures at Rabbit Key Basin to levels not significantly different from controls and outside controls. Although differences in sugar, starch, and total carbohydrate concentrations among treatments at St. Joseph's Bay were not significant, fine mesh enclosures appeared to recover more slowly at this site.

Summer 1994- Although St. Joseph's Bay and Rabbit Key Basin were sampled in fall 1994, the last sampling period with data from all three remaining sites was summer 1994. At that time, significant differences among sites were noted for all parameters sampled. In contrast, of all the parameters sampled, only ADH activities exhibited significant differences among treatments at that time (Table 6-1).

Reversing the trend of fall 1993 and spring 1994, ADH activity at the Corpus Christi site was significantly higher

than at the other two sites in summer 1994 (Table 6-2). In fact, ADH activities at Corpus Christi increased steadily from spring (summer) 1993 to summer 1994, while activities at Rabbit Key and St. Joseph's Bay were generally high in spring 1993 and spring 1994 and low in fall 1993 and summer 1994. Protein concentrations were significantly higher and starch concentrations were significantly lower at St. Joseph's Bay than at the other two sites.

Normalized ADH activity and starch concentrations exhibited similar variations among treatments. Values were highest for outside controls and significantly lower for coarse mesh enclosures. Levels in recovering fine mesh enclosures were not significantly lower than values in outside controls. Sugar concentrations and raw ADH activity were lower in control enclosures than in outside controls, but only the difference in ADH activity was significant. Protein concentrations were remarkably uniform among treatments at each site in summer 1994.

The significant difference in ADH activity among treatments apparently reflects the impact of outside controls and a repeating pattern of insignificant differences for all three sites (Fig. 6-7). At each site, outside controls had the highest ADH activity and coarse mesh enclosures had the lowest. ADH activities in recovering fine mesh enclosures at Rabbit Key Basin and St. Joseph's Bay were as high as those of control enclosures.

Pore Water Sulfide Concentrations- Pore water sulfide (PWS) concentrations varied significantly among sites for all but the last quarterly sample of this study (Table 6-4). Significant interaction of site and treatment effects occurred for four sequential quarterly samples (fall 1993 through summer 1994), but treatment effects alone were significant for only one quarterly sample (winter 1993). ANOVA results for site effects, in particular, reflect the variable number of sites sampled each quarter (Table 6-4.B.).

At the beginning of the experiment, there was almost a twenty-fold difference between PWS concentrations St. Joseph's Bay and Sunset Cove (Table 6-4). In general, the two Florida Bay sites had high PWS concentrations, while the other two sites had low PWS concentrations. By the end of the experiment, however, Florida Bay (RKB) PWS values were only 50% higher than PWS concentrations for St. Joseph's Bay.

When PWS concentrations for all sites were averaged in spring and summer 1993, there were no significant differences among treatments (Table 6-4). In fall 1993, a significant treatment effect results from extremely high PWS values in control enclosures at Rabbit Key Basin (Fig. 6-10) possibly as the result of a severe phytoplankton bloom which occurred at that time.

Significant treatment effects occurred in winter 1993, as well as in spring and summer 1994. For these three quarterly samples, PWS values were significantly higher in coarse and fine mesh enclosures than concentrations in control enclosures and outside controls, despite the fact that screens had been removed from fine mesh enclosures after sampling in fall 1993. When PWS concentrations for each site are considered separately (Fig. 6-11), significant treatment effects for spring and summer 1994 result from large differences among treatments at Rabbit Key Basin, no significant differences at Corpus Christi Bay, and marginally significant differences at St. Joseph Bay. Elevated PWS values for St. Joseph Bay outside controls in summer 1994 were caused by sea urchin grazing and other factors discussed below. By fall 1994, when only Rabbit Key Basin and St. Joseph Bay sites were sampled, treatment effects were no longer significant.

In previous studies (Carlson et al. 1994), we have found that PWS concentrations in Florida Bay seagrass beds are generally lowest in spring, increase from spring through summer, peak in fall, and decline through winter. Rabbit Key Basin and Sunset Cove PWS values follow that trend fairly well (Table 6-4, Fig. 6-12). PWS values at Corpus Christi Bay and St. Joseph's Bay, however, increased steadily during the course of the experiment.

A number of factors might have contributed to the steady increase in PWS concentrations at St. Joseph's Bay. Outside control PWS values jumped between spring 1994 and summer 1994 as the result of urchin grazing impacts. The trend continued for all treatments at St. Joseph's Bay during summer and fall, possibly as the

result of torrential rainfall in the Florida Panhandle during this period. Salinity dropped to less than 10 ppt at the head of St. Joseph's Bay and organic color stained surface water dark brown through much of the summer and fall. PWS values for each site also might have been affected by removing the tops of fine mesh enclosures in fall 1993.

TABLE 6-1: Analysis of Variance for All Sites. Data are F-Ratios, and significant effects are noted by asterisks.

Physiological Parameter	Independent Variable	Fall 1993	Spring 1994	Summer 1994
ADH Activity	Site	5.00**	3.72*	2.98
(umol/min/g FW)	Treatment	11.67***	6.43***	3.27*
	Site x Tmt	1.96	1.73	1.02
Normalized ADH	Site	2.52	5.55**	5.19**
(umol/min/mg	Treatment	4.54**	6.91***	3.75*
protein)	Site x Tmt	1.37	3.21*	0.67
Protein	Site	7.71**	8.88**	33.27***
(mg/g FW)	Treatment	3.21*	1.13	0.98
	Site x Tmt	0.94	2.40	1.06
Extr. Sugar	Site	19.61***	12.14***	0.97
(mg/g FW)	Treatment	63.83***	5.14**	2.35
	Site x Tmt	3.75**	0.83	1.19
Extr. Starch	Site	14.61***	1.92	5.10**
(mg/g FW)	Treatment	15.48***	2.52	1.02
	Site x Tmt	1.35	0.76	0.97
Sugar+Starch	Site	18.90***	5.29**	3.06
(mg/g FW)	Treatment	30.25***	3.90*	1.56
	Site x Tmt	1.61	0.84	1.09
		* P< 0.05	** P< 0.01	***P< 0.001

TABLE 6-2: Comparison of Physiological Parameters Among Sites. Data are mean values for each parameter. Values with the same letter subscript are not significantly different.

Physiological Parameter	Site	Spring 1993	Fall 1993	Spring 1994	Summer 1994
ADH Activity	Corpus Christi	0.69 c	1.17 c	1.89 b	3.54 a
(umol/min/g FW)	Rabbit Key	3.46 a	2.03 ab	3.43 a	2.03 b
	St. Joseph	3.44 a	2.68 a	3.35 a	1.91 b
	Sunset Cove	1.72 b	1.45 bc		
Normalized ADH	Corpus Christi	0.66 b	0.78 b	1.32 b	2.95 a
(umol/min/mg	Rabbit Key	2.61 a	1.81 a	2.00 ab	2.35 a
protein)	St. Joseph	2.06 a	1.91 a	2.59 a	0.98 b
	Sunset Cove	1.11 b	1.59 ab		
Protein	Corpus Christi	1.16 c	1.47 ab	1.25 b	1.12 b
(mg/g FW)	Rabbit Key	1.40 bc	1.28 b	1.80 a	0.88 b
	St. Joseph	1.75 a	1.58 a	1.36 b	2.20 a
	Sunset Cove	1.57 ab	1.02 c		
Extr. Sugar	Corpus Christi	9.94 c	12.47 b	7.68 b	28.51 a
(mg/g FW)	Rabbit Key	32.47 a	22.03 a	25.83 a	23.58 a
	St. Joseph	24.70 b	14.77 b	19.05 a	20.06 a
	Sunset Cove	12.27 c	7.55 c		
Extr. Starch	Corpus Christi	22.09 c	29.22 b	25.66 a	39.86 a
(mg/g FW)	Rabbit Key	51.40 a	49.01 a	30.05 a	45.09 a
	St. Joseph	35.94 b	31.70 b	32.85 a	16.51 b
	Sunset Cove	42.13 ab	20.89 b		
Sugar+Starch	Corpus Christi	32.03 c	41.70 bc	33.34 b	68.37 a
(mg/g FW)	Rabbit Key	83.86 a	71.04 a	64.87 a	68.67 a
	St. Joseph	60.63 b	45.74 b	51.90 a	36.57 a
	Sunset Cove	54.40 b	28.45 c		

TABLE 6-3: Comparison of Physiological Parameters Among Treatments. Data are mean values for each parameter averaged for all sites. Values with the same letter subscript are not significantly different. Sampling at Sunset Cove site ended fall 1993. Tops of fine mesh cages removed after fall 1993 sampling.

Physiological Parameter	Site/ Treatment	Fall 1993	Spring 1994	Summer 1994
ADH Activity	Outside Control	3.31 a	3.89 a	3.87 a
(umol/min/g FW)	Control	2.89 a	3.88 a	2.13 b
	Coarse Mesh	1.42 b	1.76 b	1.32 b
	Fine Mesh	1.18 b	2.96 a	2.36 ab
Normalized ADH	Outside Control	2.30 a	2.98 a	3.37 a
(umol/min/mg	Control	2.08 a	2.42 ab	1.96 ab
protein)	Coarse Mesh	1.78 ab	1.12 c	0.98 b
	Fine Mesh	0.94 b	1.98 b	2.00 ab
Protein	Outside Control	1.46 a	1.39 a	1.46 a
(mg/g FW)	Control	1.47 a	1.59 a	1.23 a
	Coarse Mesh	1.11 b	1.47 a	1.50 a
	Fine Mesh	1.33 ab	1.63 a	1.32 a
Extr. Sugar	Outside Control	43.11 a	26.93 a	31.17 a
(mg/g FW)	Control	23.76 b	22.24 ab	22.70 a
	Coarse Mesh	10.38 c	12.15 c	15.86 a
	Fine Mesh	7.96 c	18.21 bc	30.10 a
Extr. Starch	Outside Control	70.51 a	41.06 a	37.38 a
(mg/g FW)	Control	44.73 b	39.44 a	35.20 a
	Coarse Mesh	33.81 bc	26.61 a	24.66 b
	Fine Mesh	24.68 c	27.83 a	39.17 a
Sugar+Starch	Outside Control	114.72 a	67.99 a	68.55 a
(mg/g FW)	Control	68.48 b	61.68 ab	57.90 a
	Coarse Mesh	44.21 c	38.76 c	40.53 a
	Fine Mesh	32.64 c	46.03 bc	69.27 a

TABLE 6-4: Sediment Pore water Sulfide Concentrations. Data are mean values for each parameter. Values with the same letter subscript are not significantly different.

Site/ Treatment	Spring 1993	Summer 1993	Fall 1993	Winter 1993	Spring 1994	Summer 1994	Fall 1994
A. Analysis of Variance- Data are F-Ratios							
Site	70.4***	129.2***	112.0***	86.96***	8.57***	6.21**	0.61
Treatment	1.97	0.67	2.35	7.05**	2.55	1.66	1.45
Site x Tmt	2.14	1.69	4.94**	7.22**	2.86*	2.75*	0.53
B. Comparisons among Sites- Data are Mean Pore water Sulfide Concentrations (uM)							
Corpus Christi	125.7c	112.9 b	104.0 c	NS	173.7 b	225.4 b	NS
Rabbit Key	450.7b	723.8 a	1276.0 a	762.8 a	297.2 a	421.0 a	464.0 a
St.Joseph's Bay	31.7c	107.5 b	57.0 c	105.7 b	107.3 b	260.5 b	364.0 b
Sunset Cove	616.2a	800.5 a	847.0 b	NS	NS	NS	NS
C. Comparison among Treatments- Data are Mean Pore water Sulfide Concentrations (uM)							
Outside	NS	NS	NS	126.2 b	133.8 b	282.1ab	314.0 a
Control	214.8a	370.0 a	701.6 a	240.6 b	145.6 b	210.7 b	249.7 a
Coarse Mesh	261.9a	418.6 a	478.1 b	608.2 a	227.4ab	238.8ab	552.0 a
Fine Mesh	272.9a	388.5 a	476.2 b	549.7 a	289.9 a	355.8 a	540.9 a

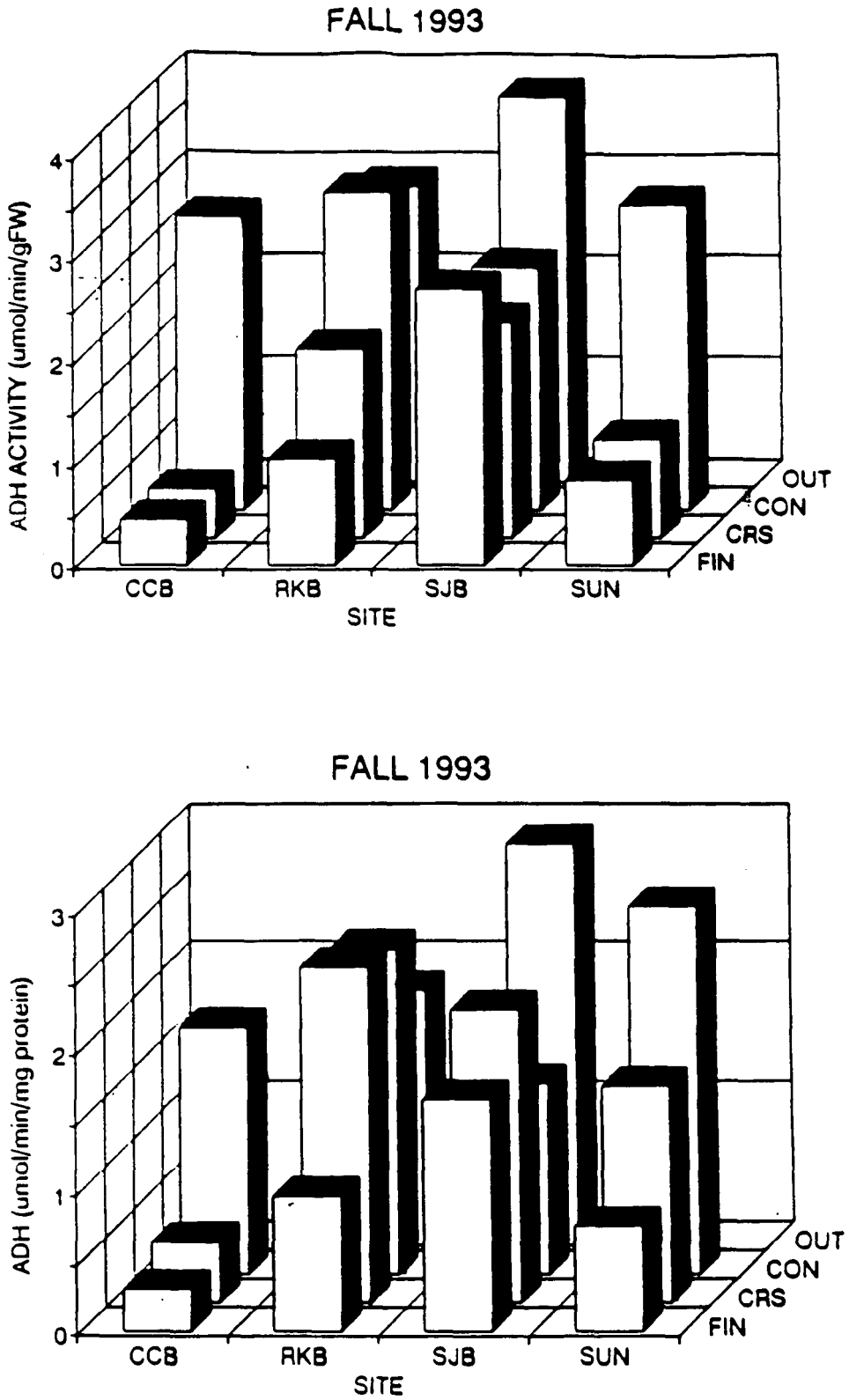
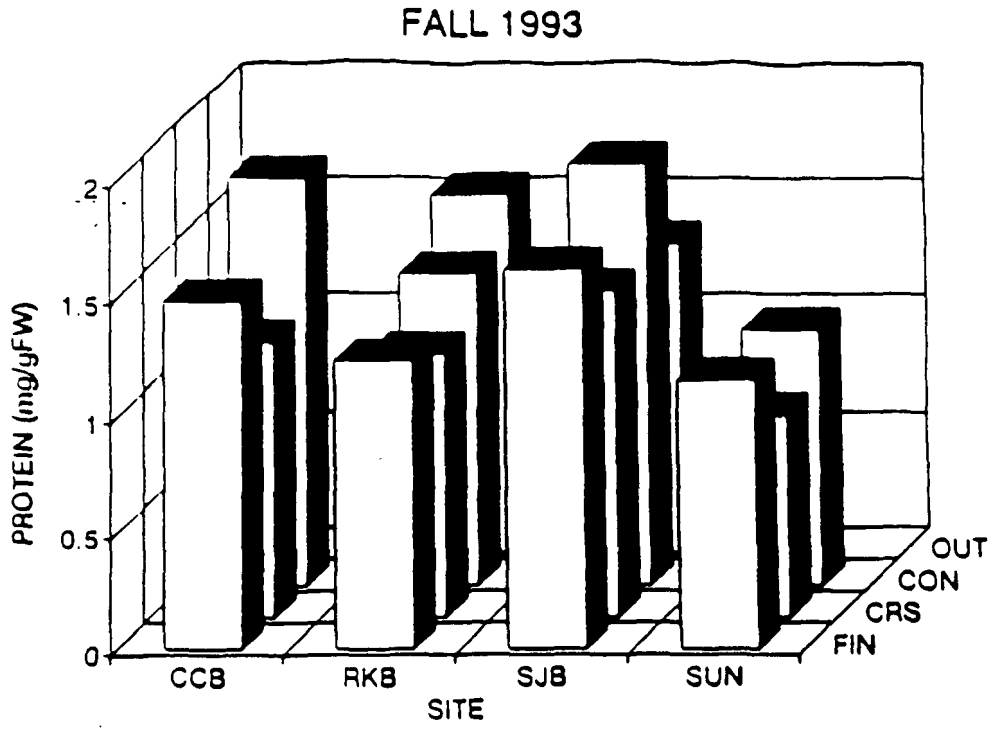


Fig. 6-1. Rhizome ADH activity for all sites, Fall 1993. Upper graph shows raw ADH activity. Lower graph shows ADH normalized to protein concentration. Site names are abbreviated on the horizontal graph axis: CCB = Corpus Christi Bay; RKB = Rabbit Key Basin; SJB = St. Joseph's Bay; SUN = Sunset Cove. Treatments are abbreviated along the right side of the graph: OUT = outside controls; CON = control enclosures; CRS = enclosures with coarse mesh; FIN = fine mesh enclosures. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($P<0.05$) different.



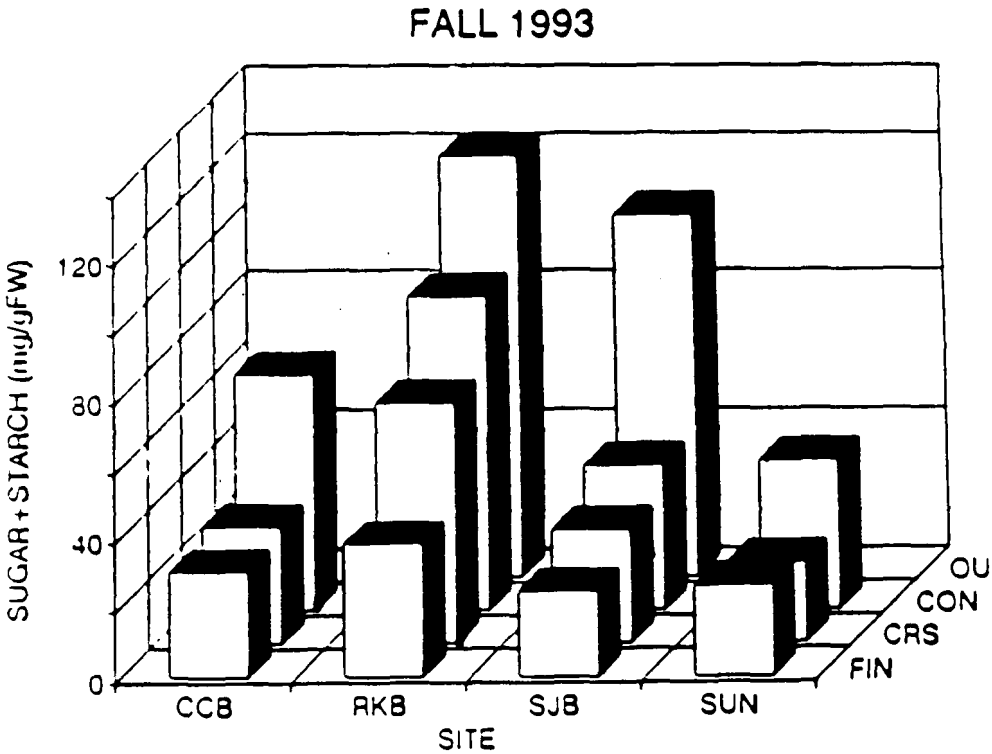
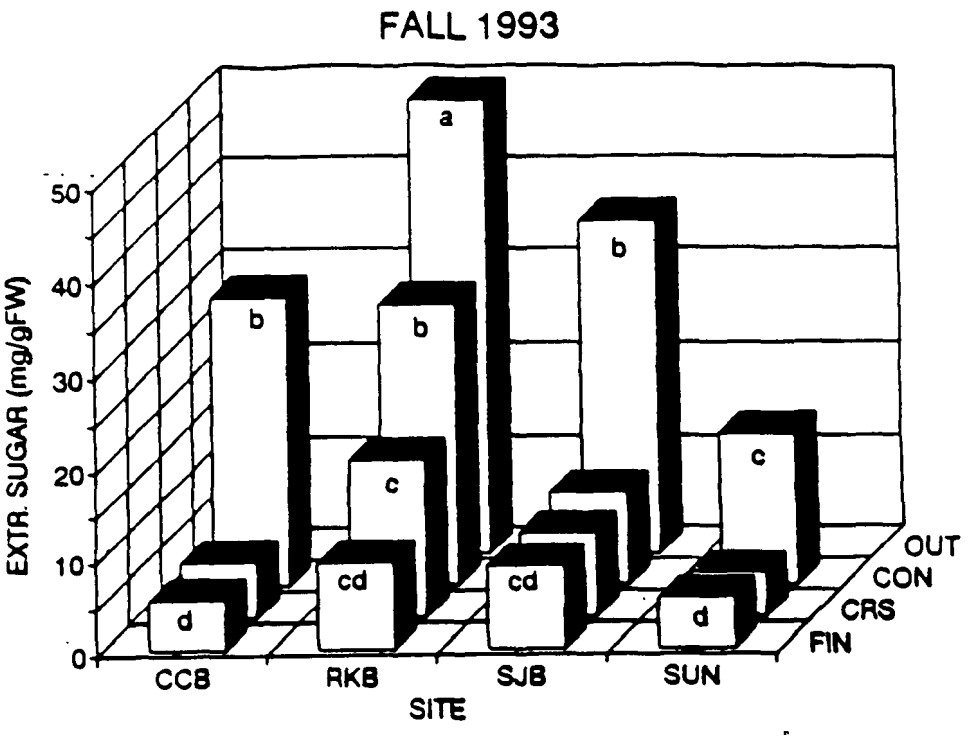


Fig. 6-2. Rhizome protein and total carbohydrate concentration, Fall 1993. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($P<0.05$) different. Abbreviations for sites and treatments are as described for Fig 6-1



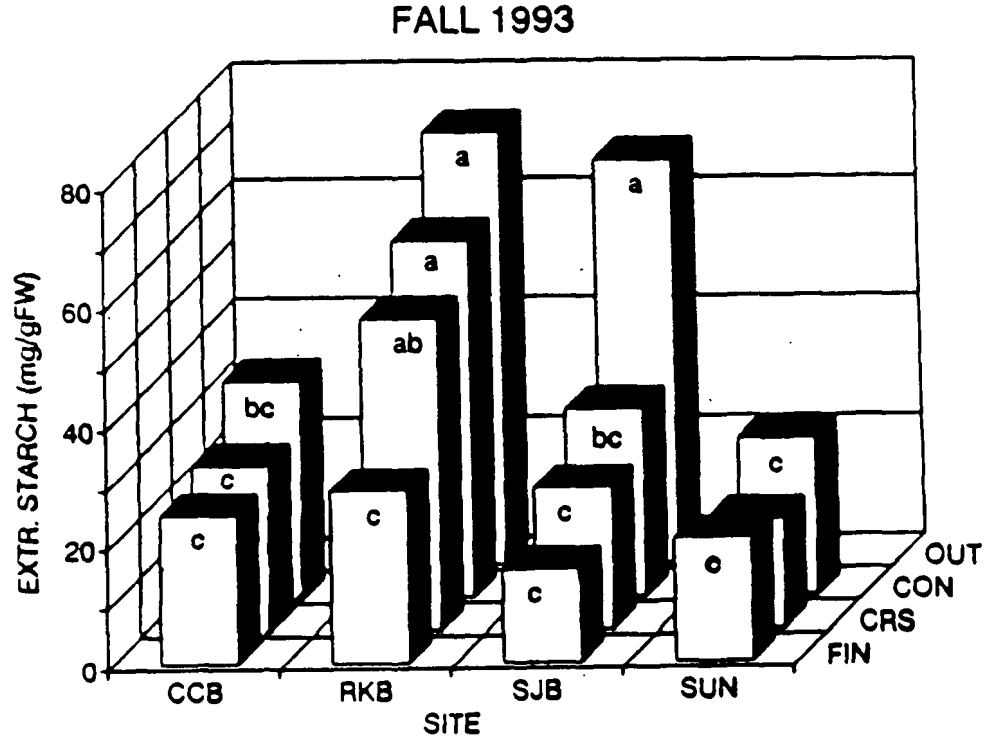
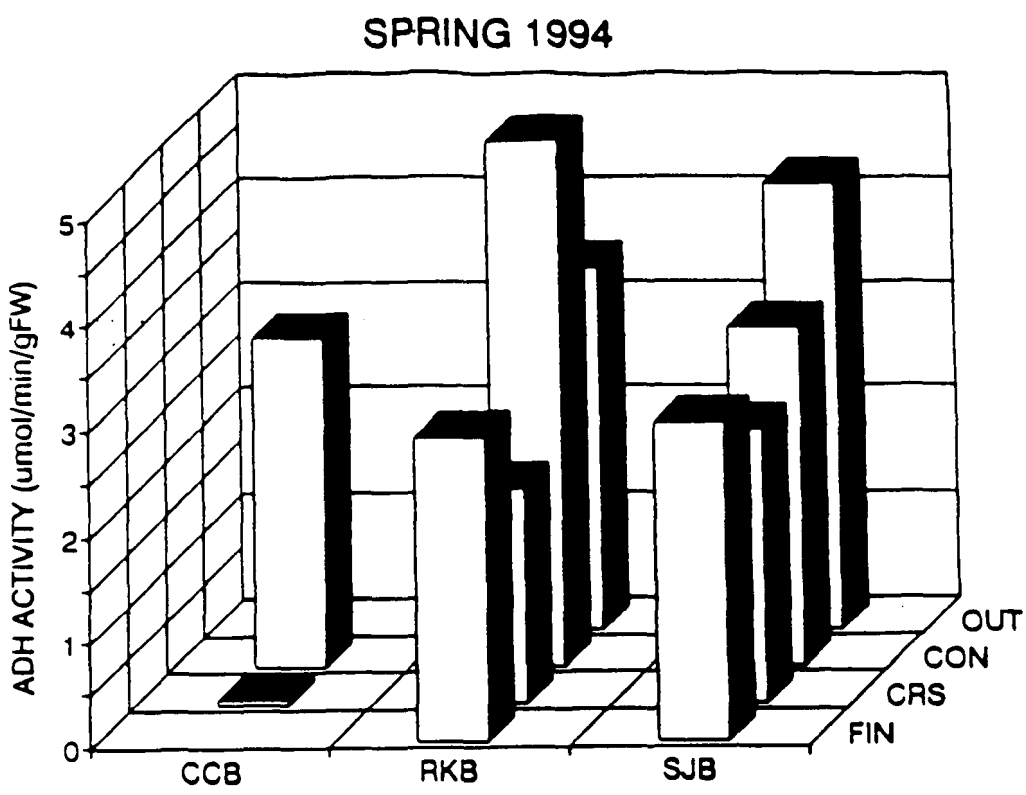


Fig. 6-3. Rhizome sugar and starch concentration, Fall 1993. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($P<0.05$) different. Abbreviations for sites and treatments are as described for Fig. 6-1.



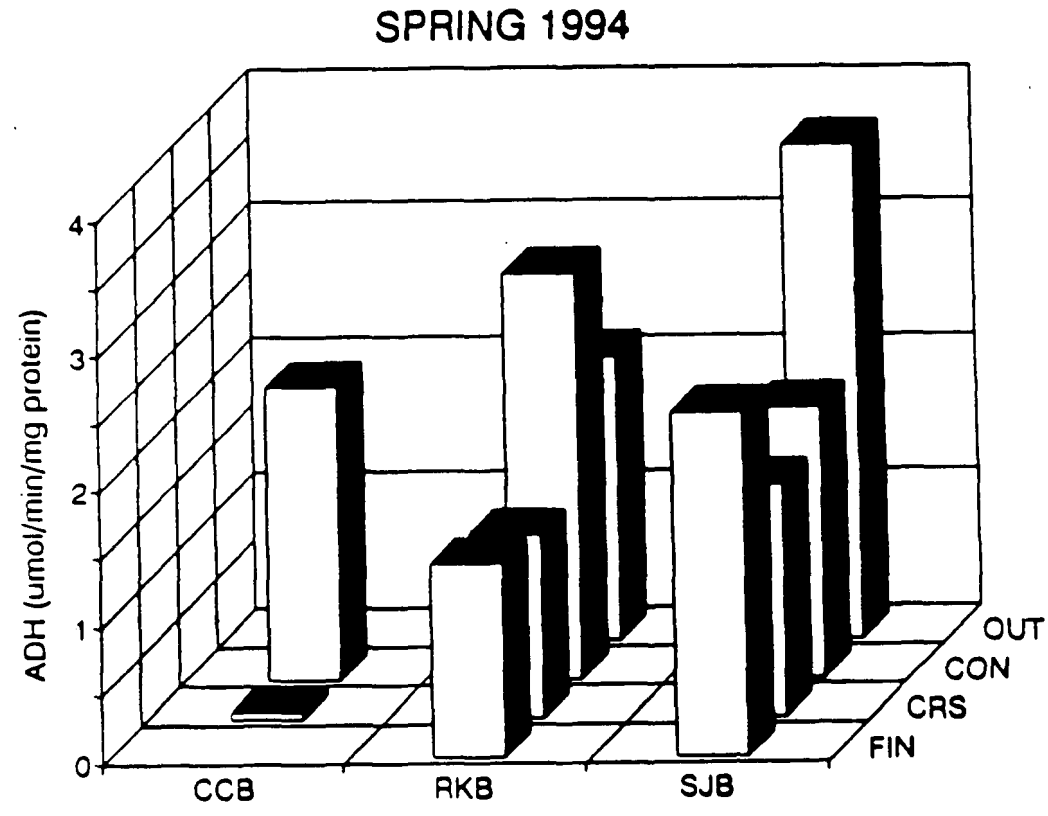


Fig. 6-4. Rhizome ADH and normalized ADH activity for all sites, Fall 1993. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($P<0.05$) different. Abbreviations for sites and treatments are as described for Fig. 6-1

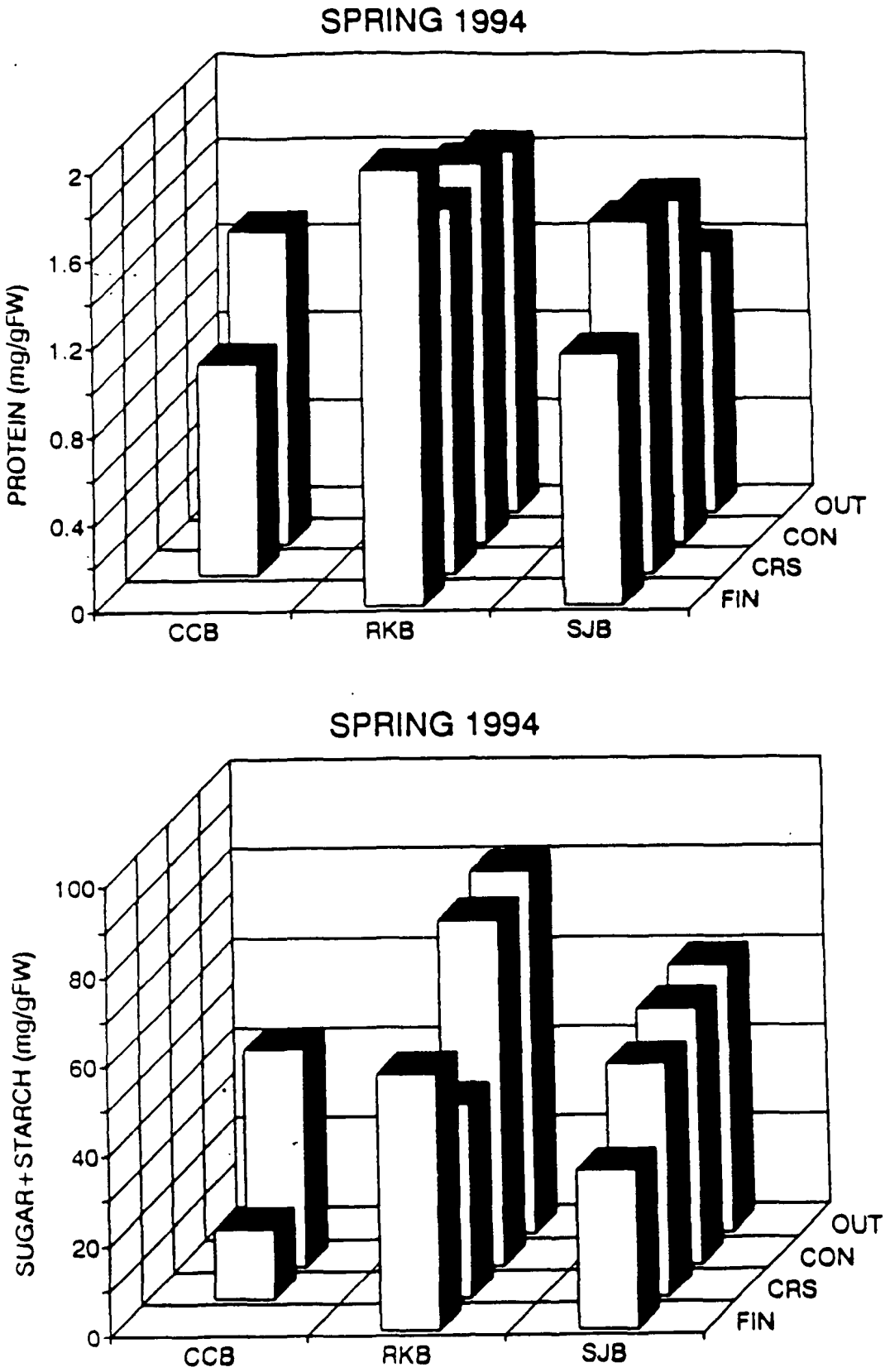


Fig. 6-5. Rhizome protein and total carbohydrate concentration, Spring 1994. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($P<0.05$) different. Abbreviations for sites and treatments are as described for Fig. 6-1

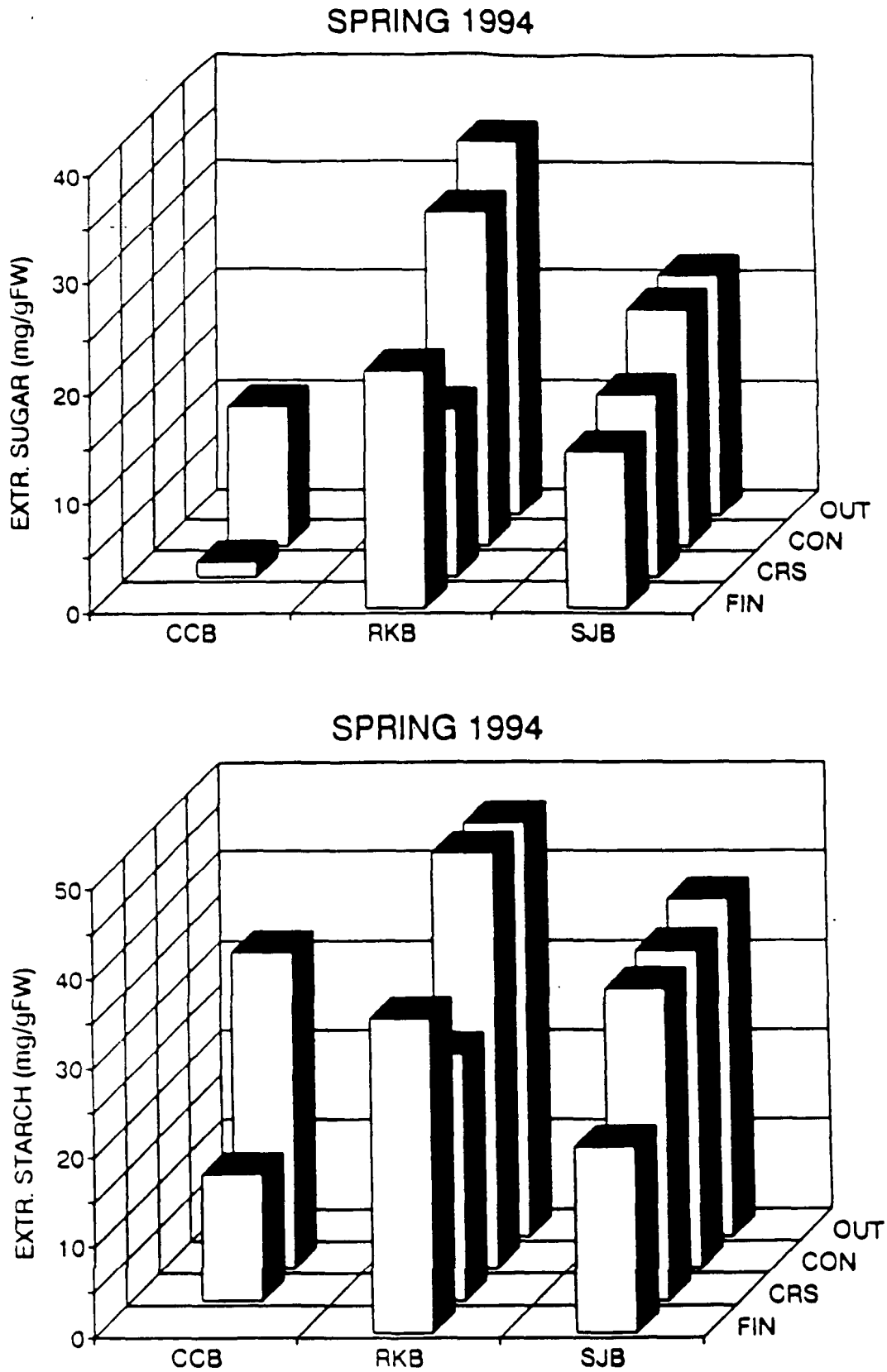
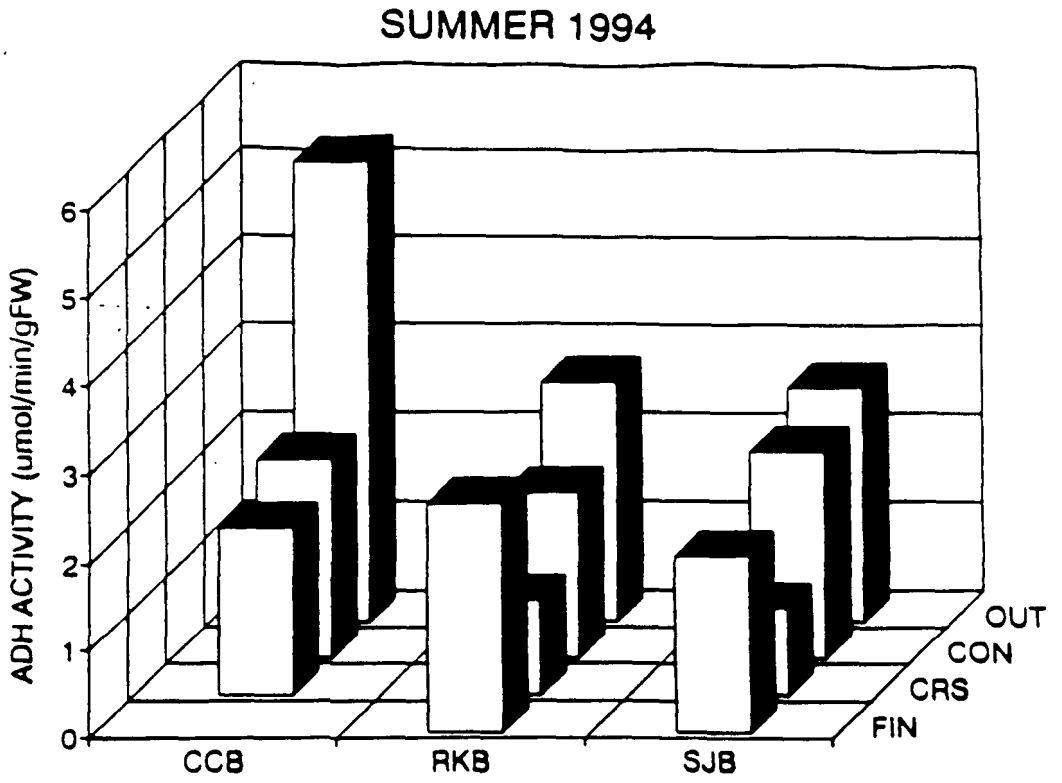


Fig. 6-6. Rhizome sugar and starch concentrations, Spring 1994. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($\underline{P}<0.05$) different. Abbreviations for sites and treatments are as described for Fig. 6-1.



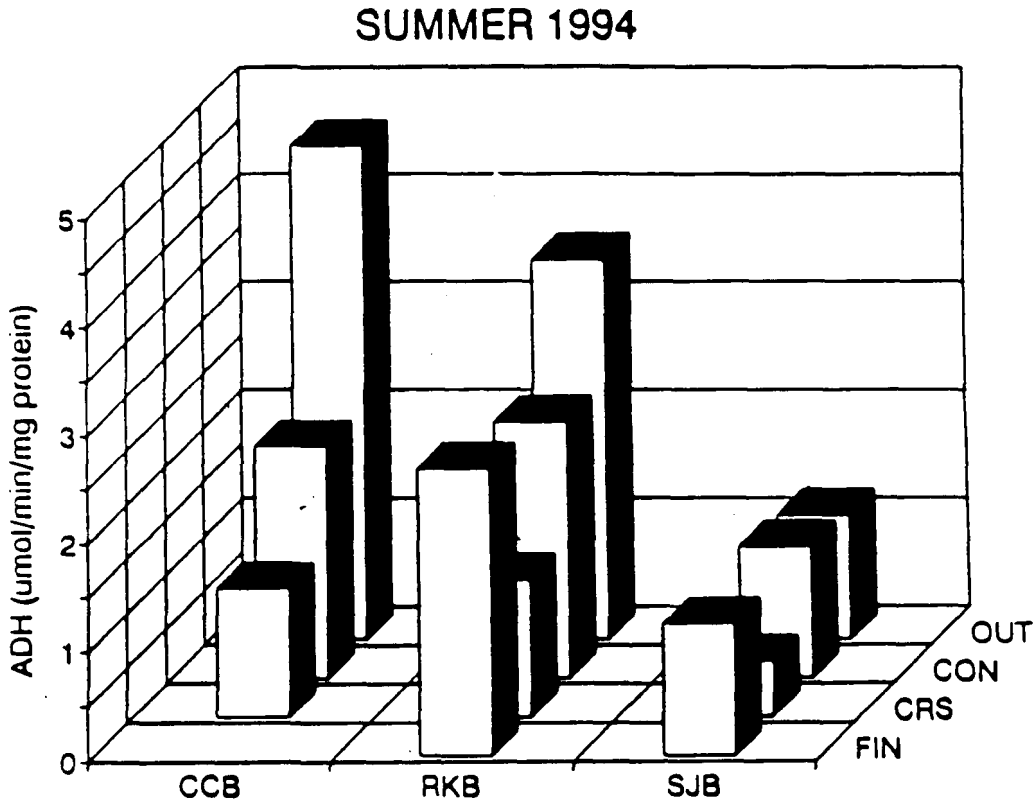


Fig. 6-7. Rhizome ADH and normalized ADH activity for all sites, Summer 1994. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($P<0.05$) different. Abbreviations for sites and treatments are as described for Fig. 6-1

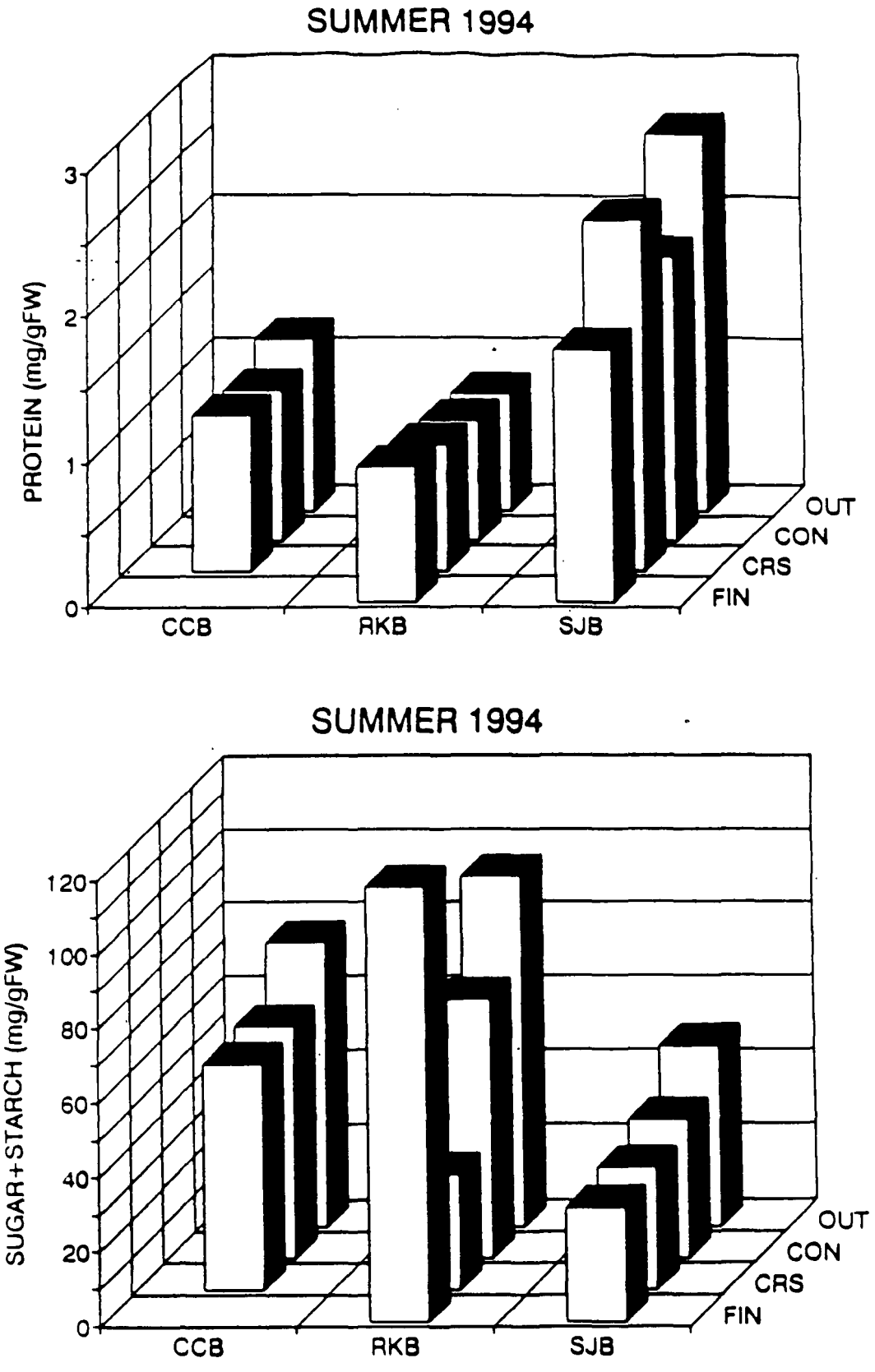
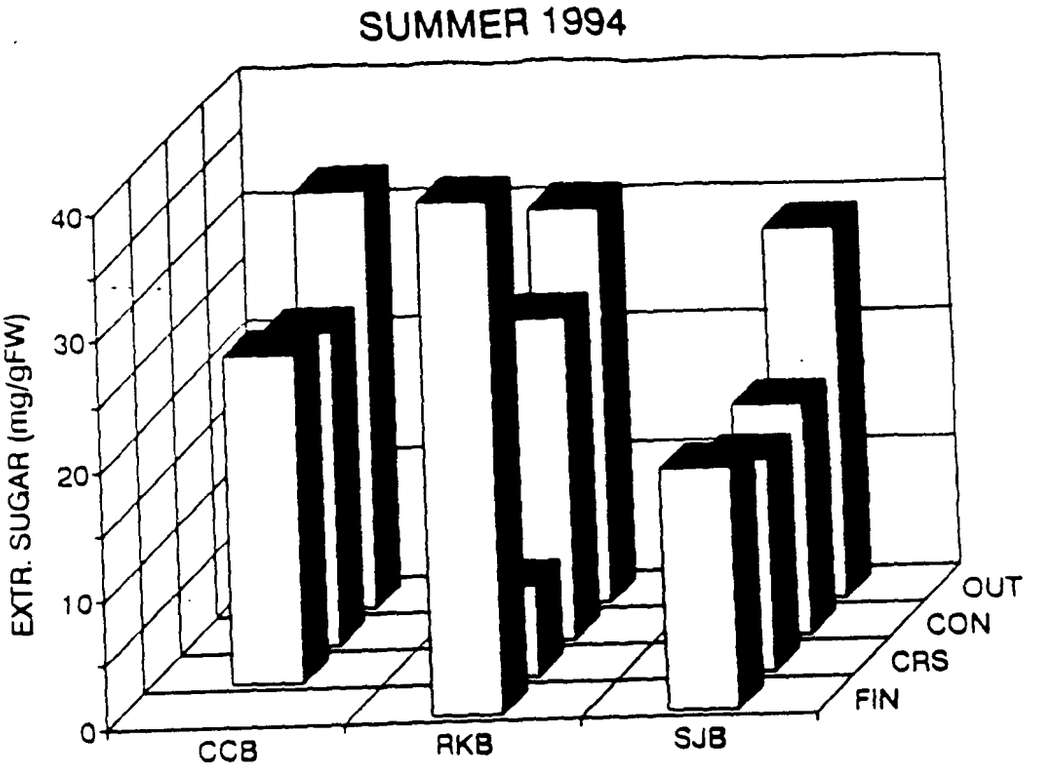


Fig. 6-8. Rhizome protein and total carbohydrate concentration, Summer 1994. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($\underline{P}<0.05$) different. Abbreviations for sites and treatments are as described for Fig. 6-1



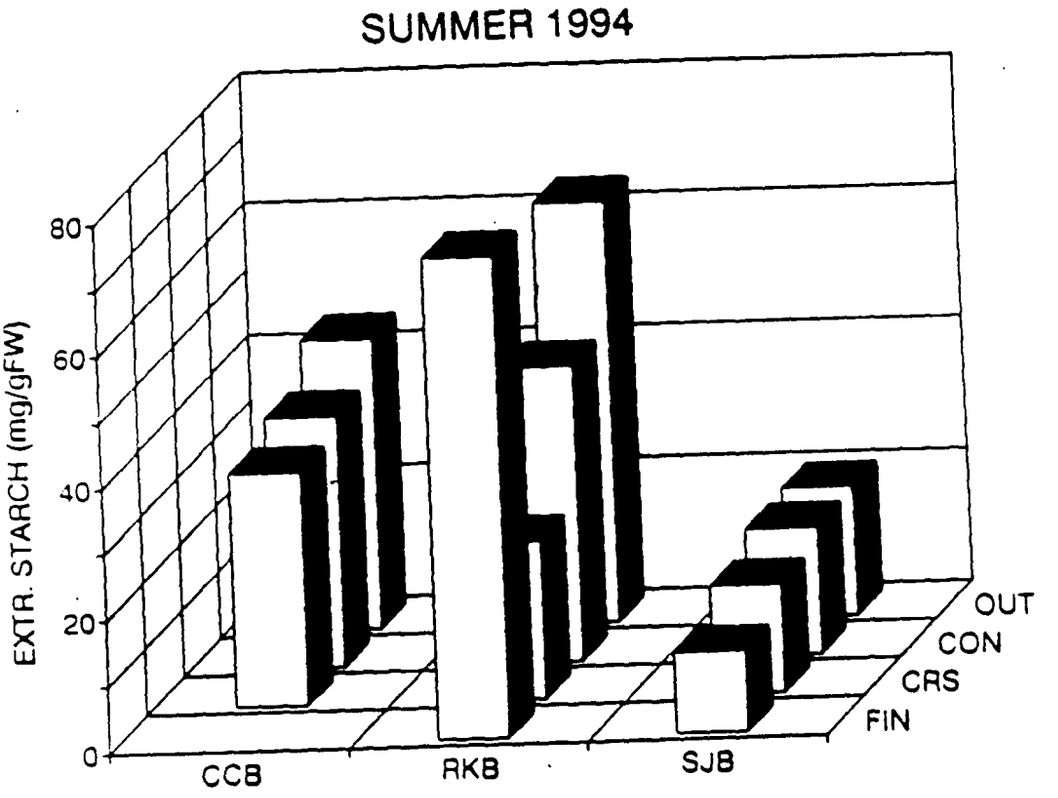


Fig. 6-9. Rhizome sugar and starch concentration, Summer 1994. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($P<0.05$) different. Abbreviations for sites and treatments are as described for Fig. 6-1.

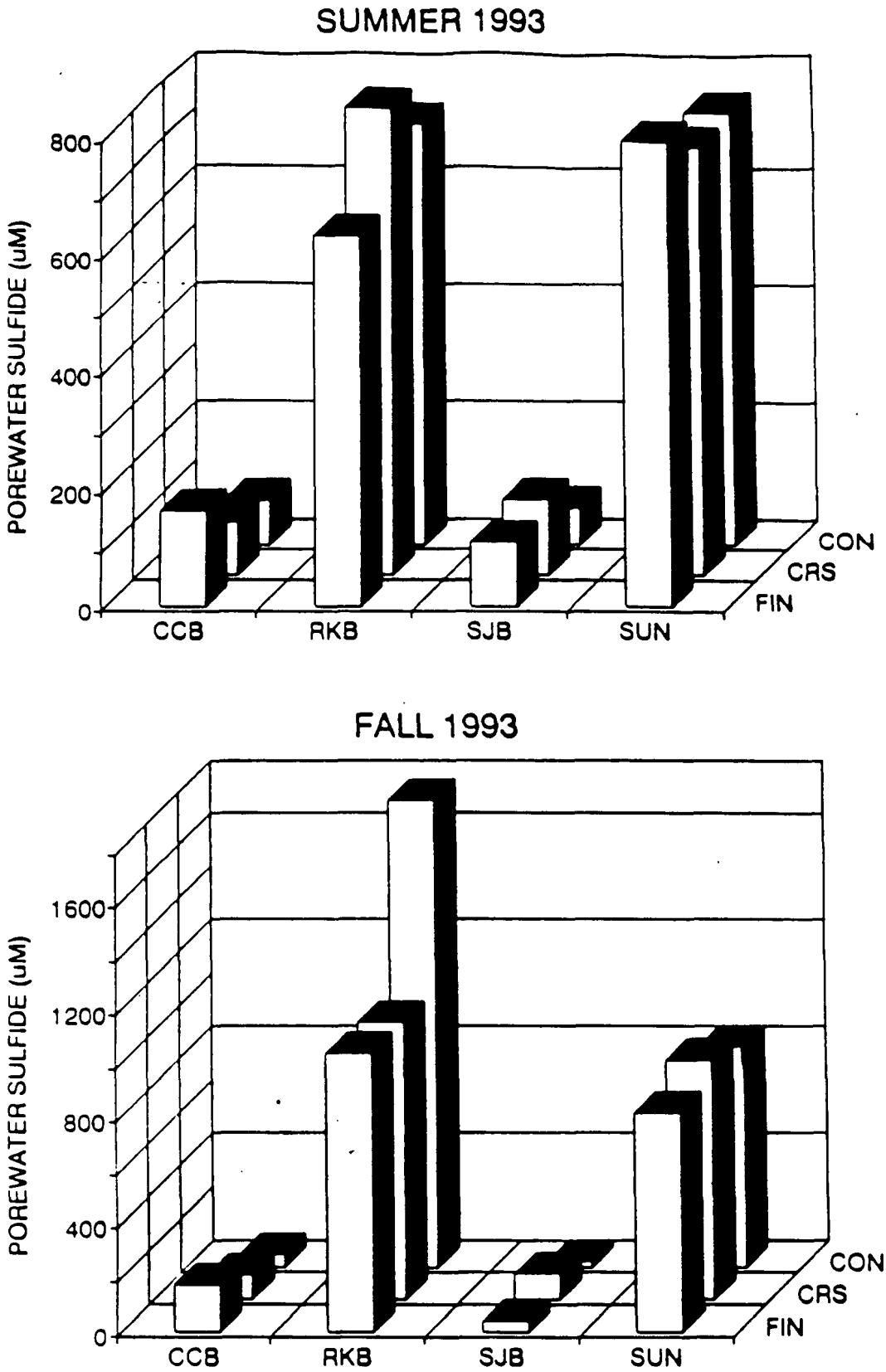


Fig. 6-10. Comparison of pore water sulfide (PWS) concentrations among sites and treatments for Summer and Fall 1993. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($\underline{P}<0.05$) different. Abbreviations for sites and treatments are as described for Fig. 6-1.

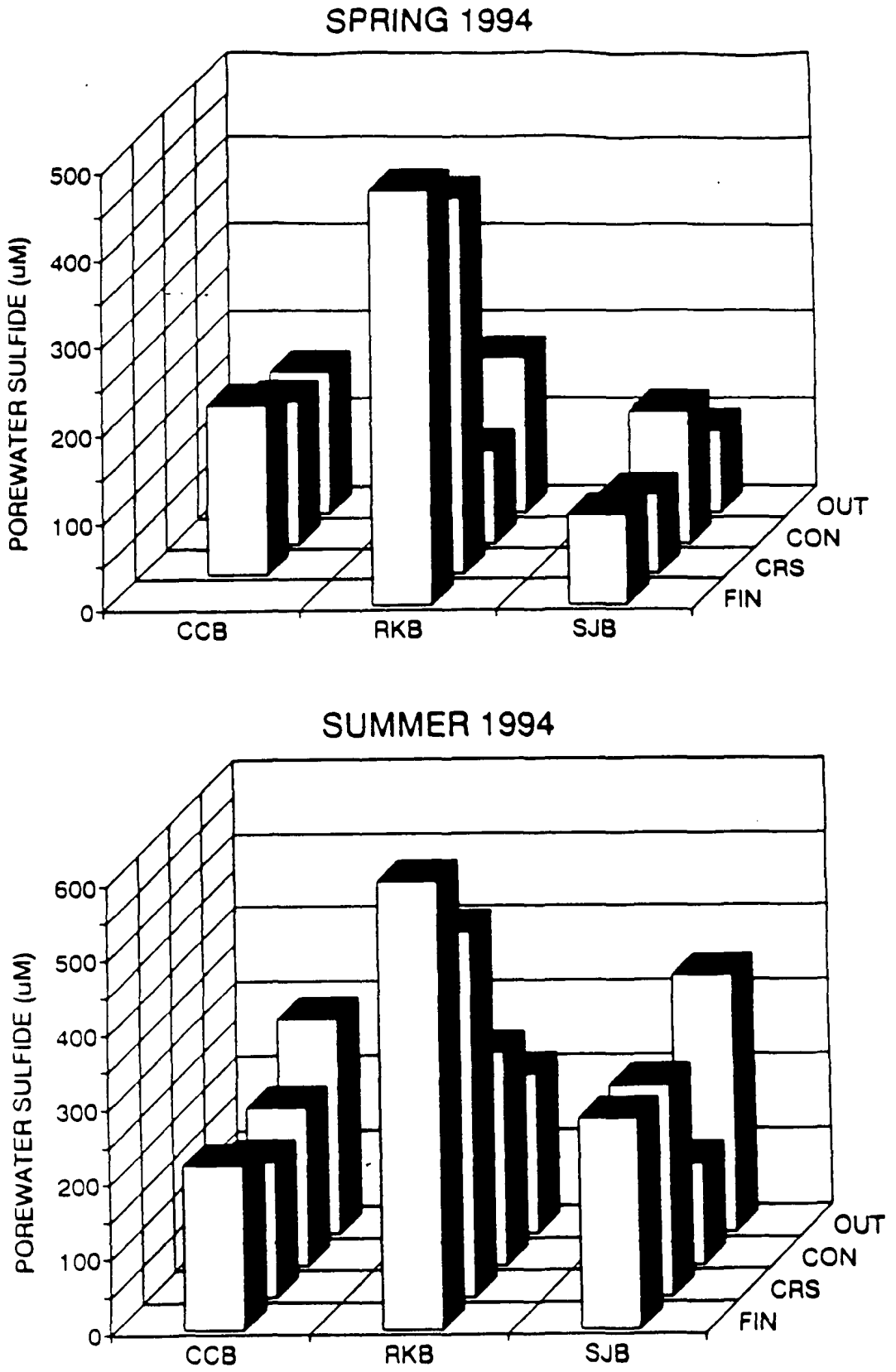


Fig. 6-11. Comparison of pore water sulfide (PWS) concentrations among sites and treatments for Spring and Summer 1994. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($P<0.05$) different. Abbreviations for sites and treatments are as described for Fig. 6-1.

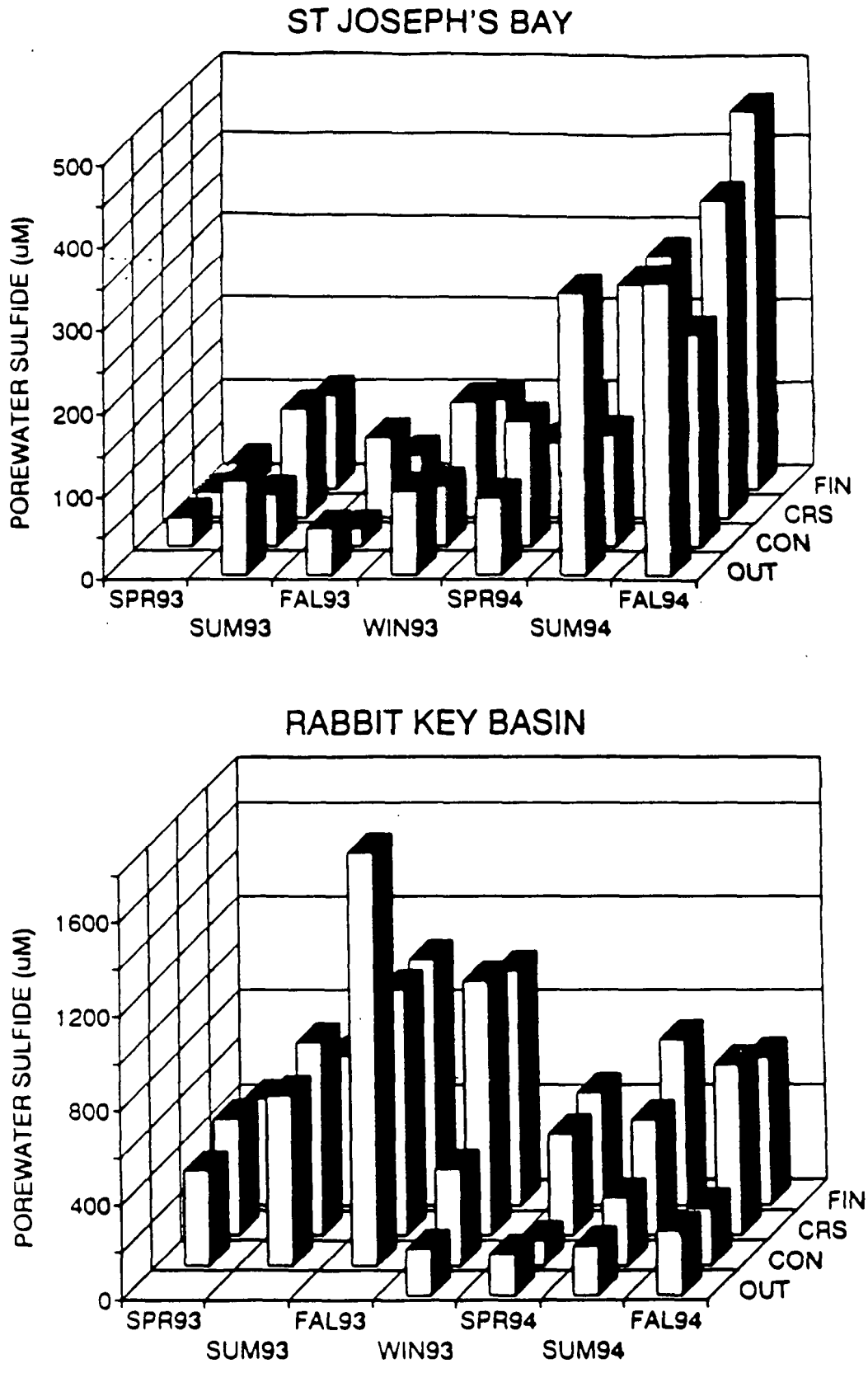


Fig. 6-12. Seasonal variation of pore water sulfide concentrations among treatments at St. Joseph's Bay and Rabbit Key Basin. Letters within or adjacent to vertical bars indicate results of multiple range tests of means; values with same letters are not significantly ($\underline{P}<0.05$) different. Abbreviations for sites and treatments are as described for Fig. 6-1.

VII. CHANGES IN PHOTOSYNTHESIS VERSUS IRRADIANCE CHARACTERISTICS OF *THALASSIA TESTUDINUM* IN RESPONSE TO SHORT-TERM LIGHT REDUCTION

Michael J. Durako and James W. Fourqurean

MESOCOSM EXPERIMENTS

The effects of short-term light reduction on the photosynthetic capacity of *Thalassia* growing in the FMRI mesocosms was assessed during July 1993 by comparing the P/I characteristics of individual 1-cm-long leaf segments from short-shoots growing in duplicate mesocosms with ambient light, 10% reduction from ambient, and 20% reduction from ambient (six mesocosms total). Four 1-gallon pots containing 4-8 short-shoots with natural sediment were used for P/I sampling (eight pots/light treatment). At each sample interval, the youngest, fully-developed leaf from a short-shoot in each of three randomly chosen treatment pots was harvested. Samples were harvested 3 days before shades were installed on the mesocosms (pretreatment), and then after 3, 6, 12, and 110 days of light reduction. Three, 1 cm long leaf segments were cut from the mid-section of each sampled leaf while submerged in a petri dish filled with ambient seawater from the mesocosms. One segment was used for the P/I measurements, the second and third segments were rinsed 3 times in DI water and placed in separate, numbered wells of multiwell plates and frozen for subsequent dry weight and chlorophyll determinations.

Leaves to be used in the P/I measurements were placed in individual wells of a 6-well multiwell culture plate containing 5 ml filtered (0.45 µm) seawater from the mesocosms. Leaf segments were removed from the multiwells in random order and placed in 2 ml of N_2-sparged filtered seawater in a well-stirred, temperature-controlled glass reaction chamber of a Hansatec DW/1 oxygen-electrode system. The Clark-type polarographic oxygen electrode was calibrated using $N_{2(gas)}$ and air-saturated filtered seawater.

Photosynthesis versus irradiance (P/I) relationships were determined for each randomly chosen leaf segment at ambient temperatures using neutral-density filters and a Kodak projector lamp. Rates of photosynthesis and respiration were measured as the change in dissolved oxygen concentration over a standardized measurement interval (2 min) in the closed (no gaseous head space) reaction chamber. For each P/I run, leaf tissues were first incubated in the dark (10-min equilibration, 2-min respiration measurement interval). The tissues were then subjected to 12 light levels (≈10 to ≈700 µE $m^{-2}s^{-1}$ photosynthetically active radiation [PAR = 400 to 700 nm] as measured by a Li-Cor 2π quantum sensor) in increasing order (1-min equilibration, 2-min photosynthetic measurement interval). At the end of each P/I run, leaf tissues were removed from the chamber, rinsed three times in deionized water, placed in a well of a multiwell plate and frozen for subsequent chlorophyll determinations. A complete P/I treatment series (three replicate/treatment x three treatments = nine runs) was run at each sample interval.

Chlorophyll was extracted by grinding leaf segments frozen by liquid N_2 in a liquid N_2-chilled mortar in 90% spectrophotometric grade acetone. Chlorophyll *a* content was then measured spectrophotometrically according to Sternan (1988). Dry weight was determined by drying leaf segments for 48 h at 60 °C. Photosynthetic and respiratory rates are expressed as µmole O_2 mg^{-1} chl a h^{-1}.

Respiration rates and the P/I characteristics α and P_{max} were determined for each P/I run (Fourqurean and Zieman, 1991). The initial slope (α) of the P/I curve, which indicates photosynthetic efficiency, was calculated by linear regression of the dark respiration rate plus the photosynthetic rates at the first four light levels. Light-saturated photosynthetic rate (P_{max}) was calculated by averaging the net photosynthetic rates at light levels >300 µE $m^{-2}s^{-1}$ PAR.

Figures 7-1 and 7-2 summarize the P/I characteristics over the 110 day experimental period. Little in the way of treatment-related trends are evident until the +12 day post-treatment sampling. At this time, all six P/I characteristics exhibited a stepwise decrease with decreasing light. After 110 days, all of the P/I characteristics in the shaded treatments were lower than at 12 days. P_{max} and I_k were also lower in the

characteristics exhibited a stepwise decrease with decreasing light. After 110 days, all of the P/I characteristics in the shaded treatments were lower than at 12 days. P_{max} and I_k were also lower in the controls, suggesting some overall stress of the plants in the mesocosms. These trends suggest that the plants may be shutting down metabolic and photosynthetic processes in response to the reduction in light. Figure 7-3, which shows the actual P/I data points after 12 days of light reduction, also illustrates this trend. The response curves in figure 7-3 were generated by fitting the data points to the hyperbolic tangent model of Jassby and Platt (1976), modified to include respiration. This figure illustrates that the segments did not reach light saturation at the intensities used here, and hence, P_{max} was underestimated. The stepwise decrease in α, P_{max}, and respiration with decreasing light, after 12 days, is partially due to the stepwise increase in chlorophyll a concentration in the leaves (Fig. 7-4). However, the same trends were observed when the P/I characteristics were calculated on a dry weight basis so the changes are more than just pigment-based.

FIELD EXPERIMENTS: Sunset Cove

The effects of short-term light reduction on the photosynthetic capacity of *Thalassia* growing in situ was assessed during September 1993 by comparing the P/I characteristics of individual 1-cm-long leaf segments from short-shoots growing in 1-m^2 treatment plots in Sunset Cove, Key Largo (25°05.34N, 80°27.057W). Triplicate plots with ambient light, approximately 10% reduction from ambient (coarse screen), and approximately 20% reduction from ambient (fine screen) were established in a random 3x3 plot design. Shade screens were attached to PVC frames with legs and were placed at a level just above the leaf canopy. At each sample interval, the youngest, fully-developed leaf from one randomly chosen short-shoot from within each of the three treatment plots was harvested. This was accomplished by cutting the leaf blade then placing it in a prelabeled ziploc bag. Time 0 samples were harvested the day the shades were installed (9/16/93), samples were then harvested as described above 3, 6, 12, and 25 days after the establishment of the treatment plots. Procedures for the P/I measurements were the same at those for the mesocosm experiments. All material was collected the morning of the P/I runs.

Figures 7-5,7-6, and 7-7 summarize the P/I characteristics and leaf chlorophyll levels over the 25 day experimental period. Unlike the mesocosm experiments, there are no treatment-related trends evident in any of the measured characteristics from Sunset Cove *Thalassia.*
This lack of treatment-induced trends may be due to the heterogeneous nature of the experimental site. Sunset Cove has experienced significant seagrass die-off so our site selection was limited to an apparently healthy patch-bed adjacent to the long term shading plots. In addition, September-October is a period of relatively high and constant water temperature, but decreasing day length. This is a time of year that may already be stressful to seagrasses possibly masking any treatment effects. This may explain the overall increasing trend in respiration rates over the 25-day experimental period.

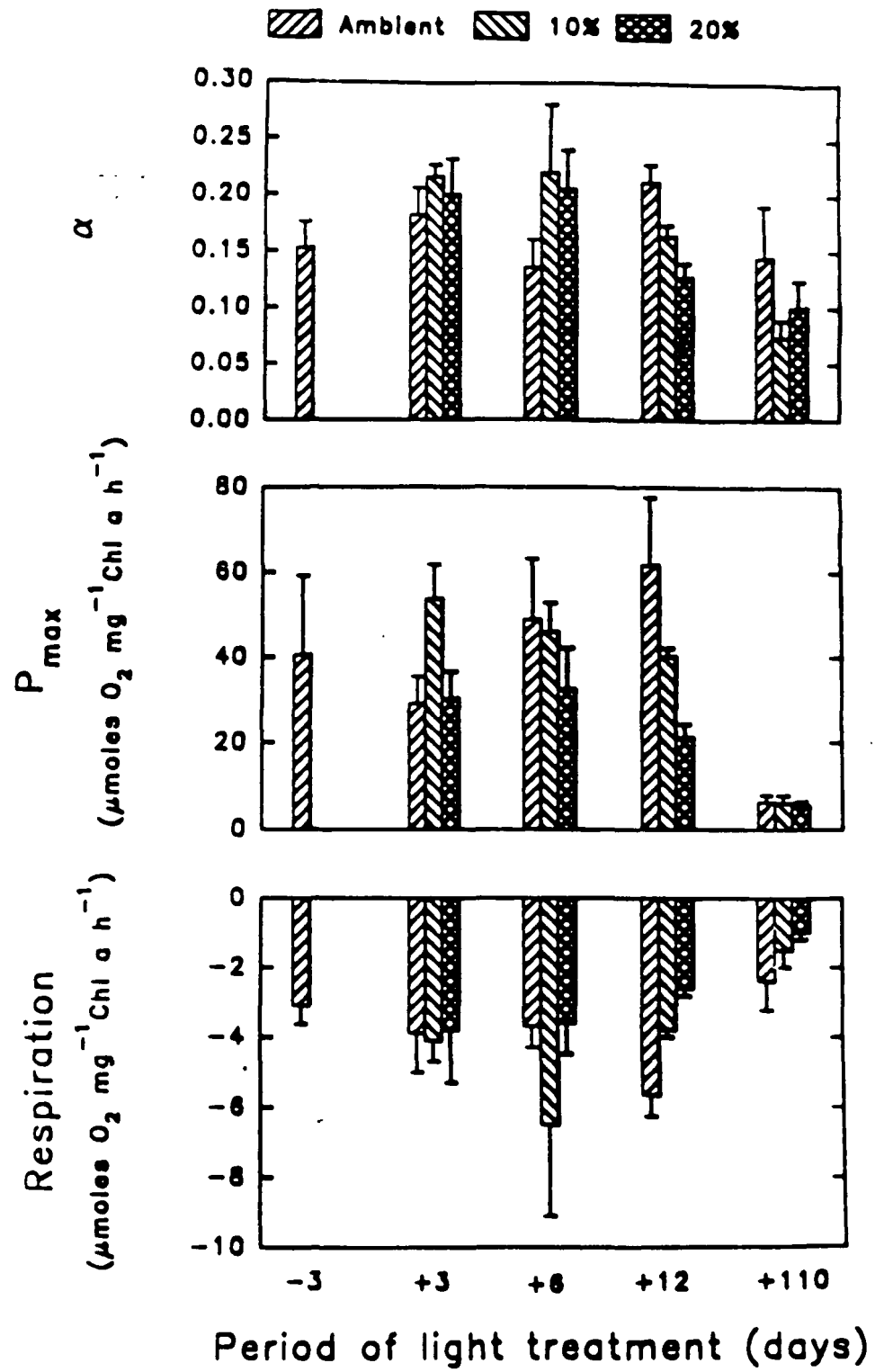


Fig. 7-1. Chlorophyll a-based photosynthesis versus irradiance characteristics (respiration, P_{max}, and α) of *Thalassia testudinum* in response to short-term light reduction in FMRI mesocosms.

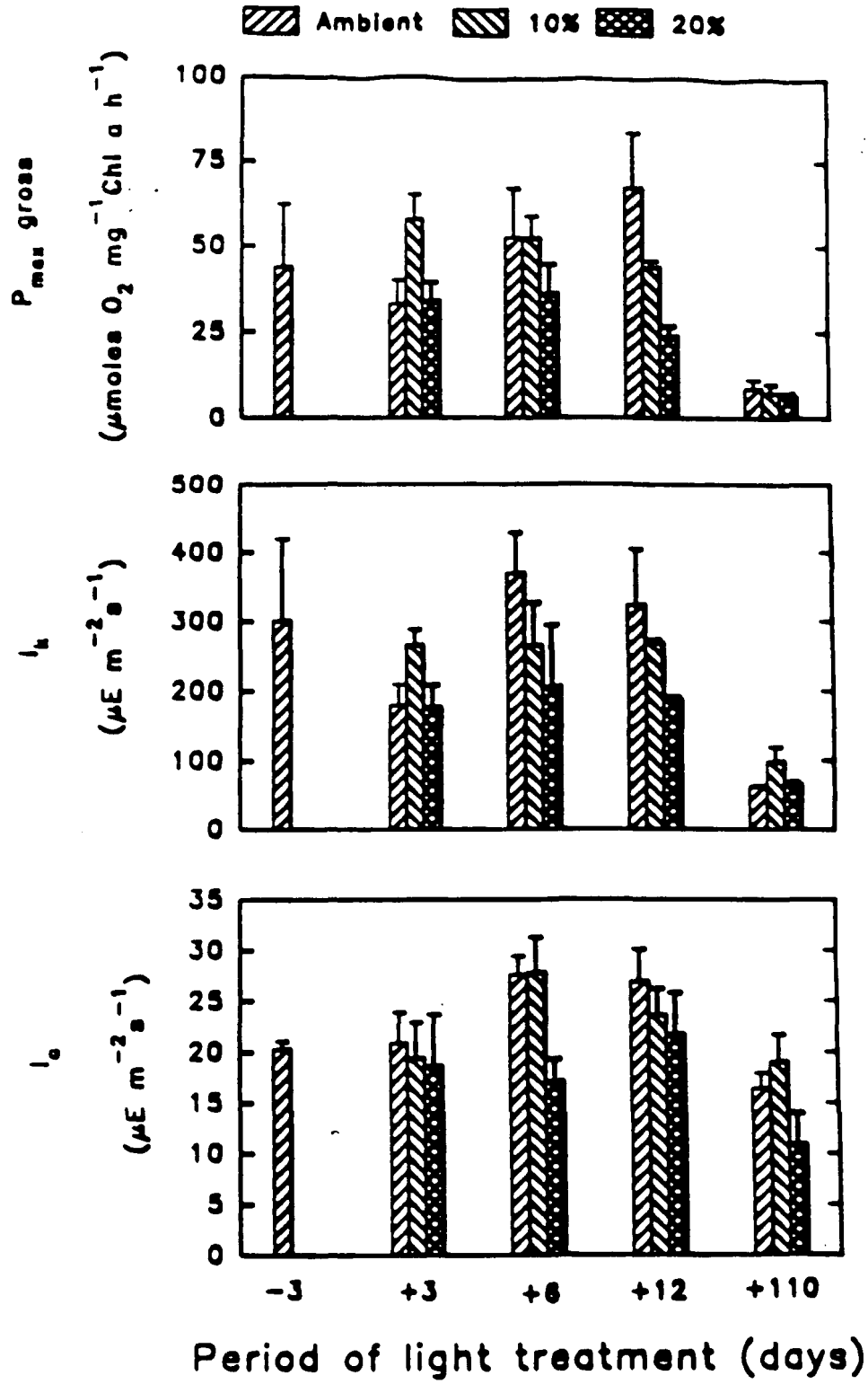


Fig. 7-2. Chlorophyll a-based photosynthesis versus irradiance characteristics (I_c, I_k, and P_{max} gross) of *Thalassia testudinum* in response to short-term light reduction in FMRI mesocosms.

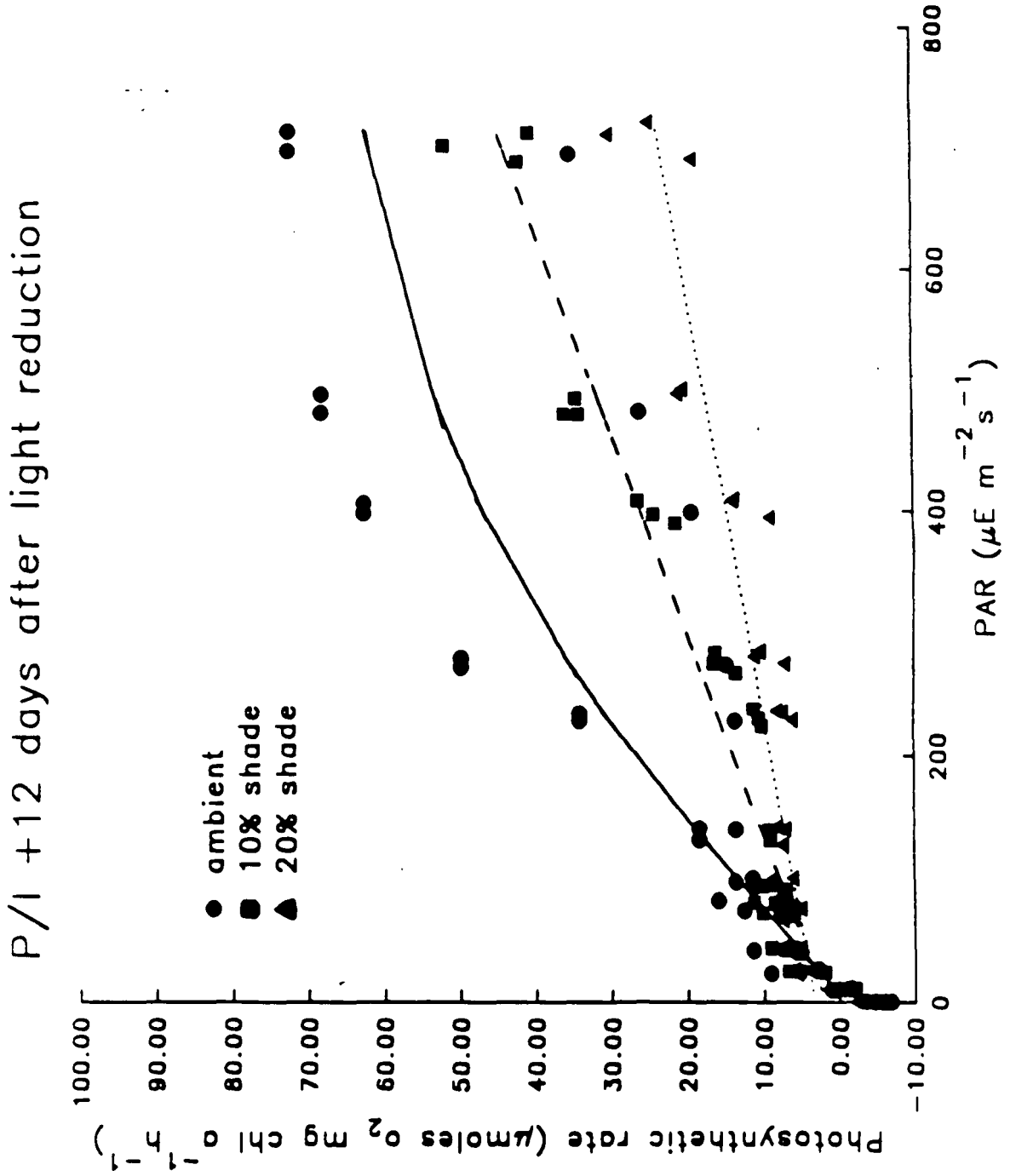


Fig. 7-3. Photosynthesis versus irradiance responses of *Thalassia testudinum* exposed to ambient light, 10% shade and 20% shade for 12 days in FMRI mesocosms.

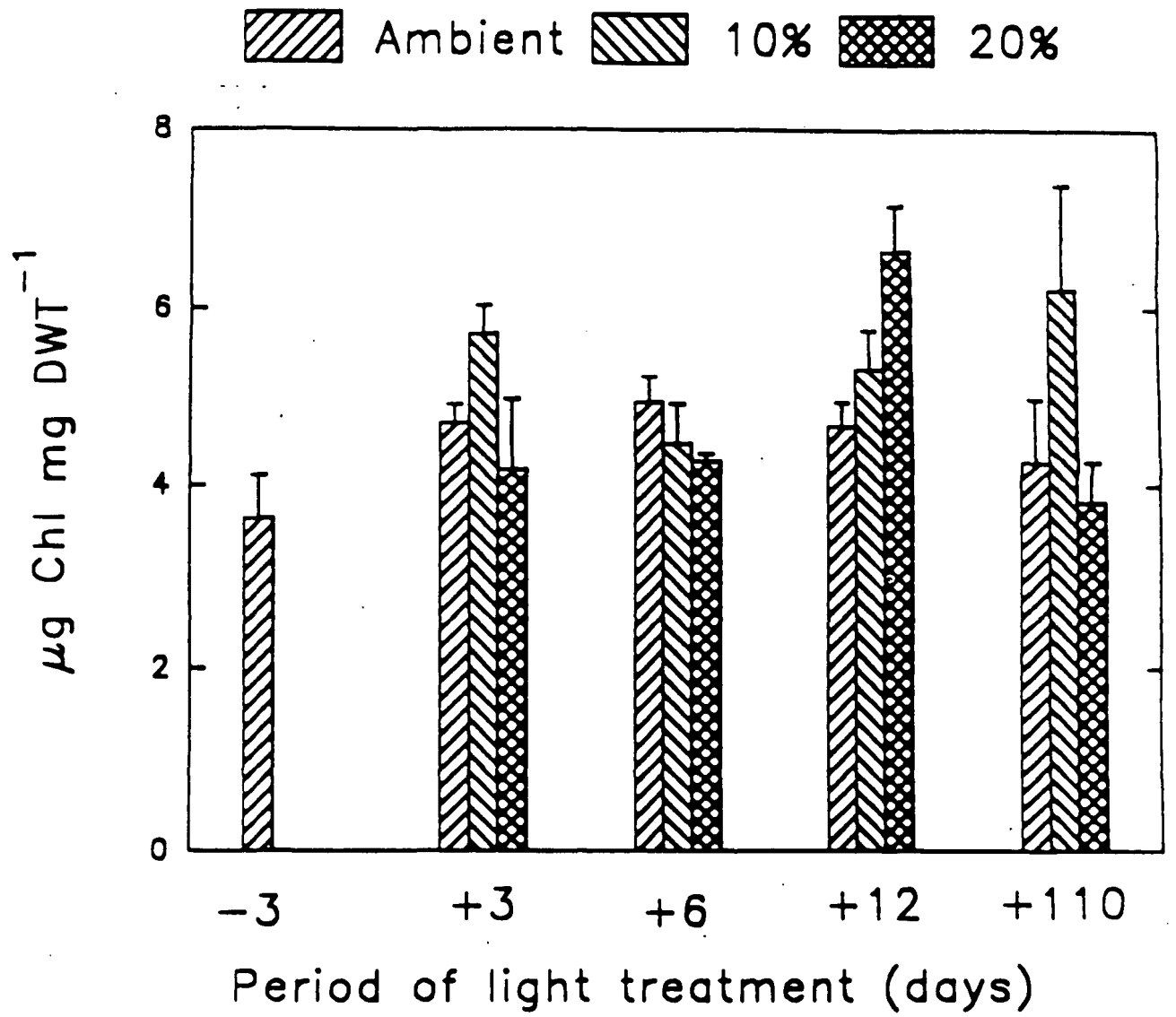


Fig. 7-4. Changes in chlorophyll a concentration of leaves of *Thalassia testudinum* in response to short- and longer-term light reduction in FMRI mesocosms.

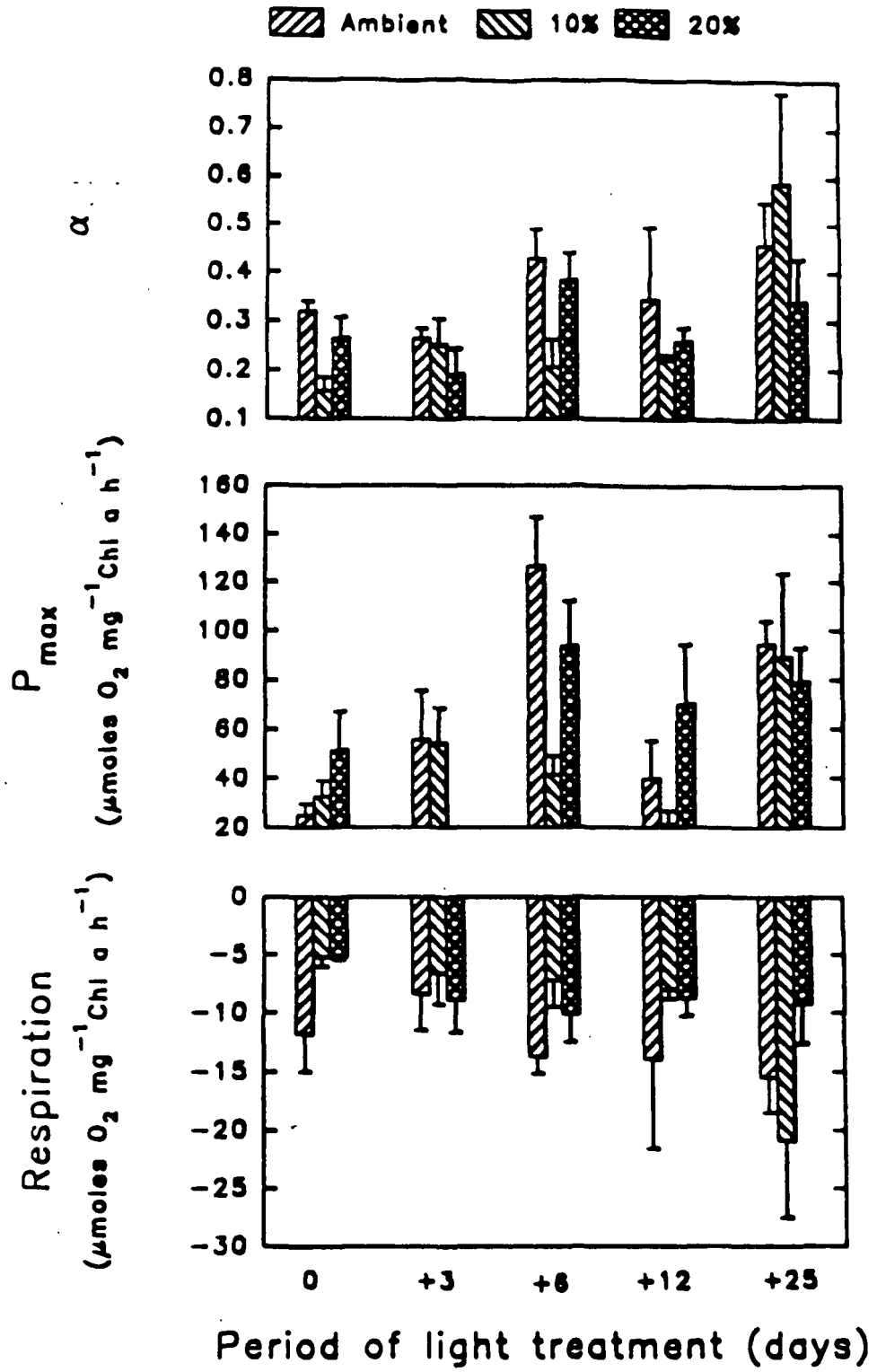


Fig. 7-5. Chlorophyll a-based photosynthesis versus irradiance characteristics (respiration, P_{max}, and α) of *Thalassia testudinum* in response to short-term light reduction in Sunset Cove, Key Largo.

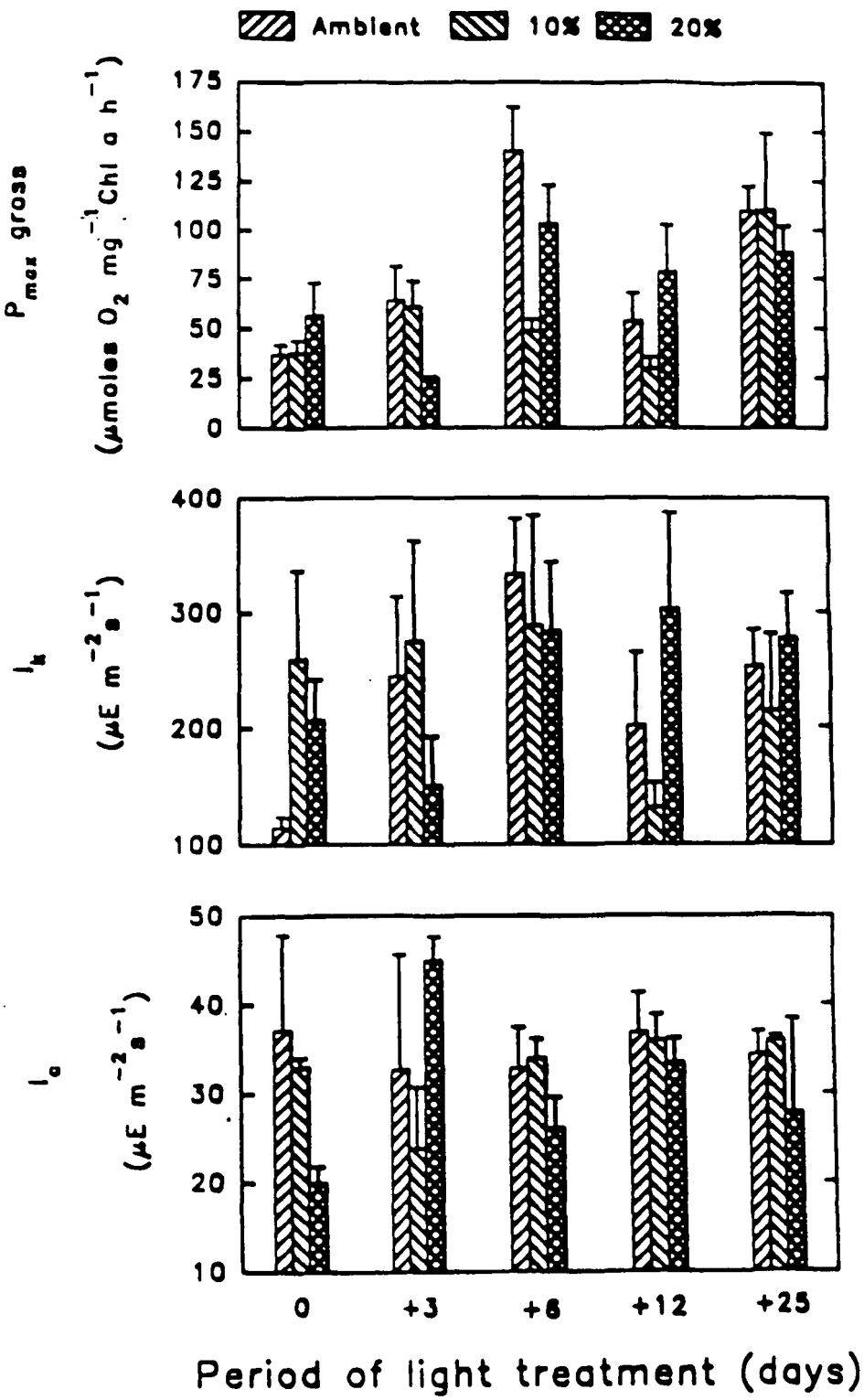


Fig. 7-6. Chlorophyll a-based photosynthesis versus irradiance characteristics (I_c, I_k, and P_{max} gross) of *Thalassia testudinum* in response to short-term light reduction in Sunset Cove, Key Largo.

VIII. SUMMARY

The carbon balance of seagrasses is more complex than that of phytoplankton or macroalgae due to the structural complexity of seagrasses (Fourqurean & Zieman, 1991). Root/shoot ratios are very important to seagrass carbon budgets because below-ground non-photosynthetic tissues must be supported by photosynthetic carbon production in the leaves. The below-ground portion of *Thalassia testudinum (turtle grass)* can account for 50 to over 90% of the total biomass (Zieman, 1982; Powell et al, 1989; Fourqurean & Zieman, 1991). Below-ground tissue is generally a photosynthate reservoir that supports growth and maintenance of other tissues during periods of low photosynthetic production (Dawes & Lawrence, 1980; Pirc, 1985) in addition to its role in anchoring the plant and the sediments and for nutrient uptake to the seagrass.

The photosynthate produced in leaf tissues and transported to subterranean tissues is critical in processes involving new shoot growth, carbohydrate storage and respiration (Ralph et al., 1992). The strong seasonal variation in stored carbon reserves in rhizome tissues are largely a function of photosynthate production in summer and the utilization of these reserves for growth and respiration in winter and early spring (Dawes & Lawrence, 1980; Pirc, 1985). Below-ground carbohydrate reserves are also critical for survival and regrowth during extended periods of light reduction and following artificial defoliation (Dawes & Lawrence, 1979; Drew, 1983; Dawes & Guiry, 1992). Since plant use of stored carbon reserves in below-ground tissues is most often related to unfavorable light conditions, decreased rhizome carbon reserves could be a reliable indicator of impending decline in seagrass distribution and biomass.

Determining potential effects of reduced light at response levels that are relatively easily measured, such as shifts in resource allocation, plant biomass and density, or effects on the associated faunal community structure, will allow us to assess changes and perhaps avoid a serious decline in seagrass populations in other locations. The primary experiments in this study utilized experimental shade treatments as an analogue to nonwavelength-specific water-quality related reduction of light to *Thalassia testudinum* meadows. Shading decreases the total amount of photosynthetically active radiation (PAR), and consequently the rates of photosynthetic carbon fixation of seagrasses. Shading may also influence seagrass carbon budgets by inducing morphological changes in the structure of the plants, or by inducing changes in the physiological response of the photosynthetic apparatus of the plant. It is not presently known if chronic light reduction affects seagrass respiration or allocation of plant resources into leaves versus non-photosynthetic structures.

Reduction in light may have short-term and long-term effects on seagrass communities, and photoadaptation may occur at both morphological and physiological levels. Plants adapted to low-light environments tend to have greater proportions of their biomass allocated to green leaves, the photosynthetic portions of the plants, at the expense of non-photosynthetic structures like roots and rhizomes. *Thalassia* from naturally occurring populations can exhibit a great deal of variation in the relative amount of biomass allocated to leaves (Fourqurean and Zieman 1991). *Thalassia* growing at the deep, light-limited edges of seagrass beds can exhibit higher leaf area indices and above-to-belowground ratios than nearby plants from higher light environments (Dawes and Tomasko 1988). *Thalassia* plants from dense meadows have a higher proportion of their biomass allocated to leaves than plants from sparse meadows as a consequence of low light from self-shading in the dense meadows (Fourqurean et al, 199).

Other typical responses of plant to shading are physiological. The photosynthesis versus irradiance (P/I) response of submerged macrophytes can change in response to changes in light availability. This physiological photoadaptation can occur quickly (in a matter of days) after the change in light availability (Goldsborough and Kemp 1988). Typically, the initial slope of the P/I curve, increases in response to shading, while the asymptotically approached maximum photosynthetic rate, Pmax, decreases., but it is unclear whether this physiological photoadaptation can occur rapidly enough in *Thalassia* to compensate for new reductions in incident light to established meadows.

Throughout the course of this project, each of the major field sites experienced one or more severe stresses, several of which are clearly chronic. Both Port Aransas and Florida Bay were heavily affected by storms in the winter and spring of 1993. Florida Bay and much of the surrounding waters were effected by massive turbidity

plumes and algal blooms resulting from the combination of seagrass dieoff and the frequent and intense storms. The 'Storm of the Century' which occurred around 12 March 1993, just prior to the initiation of this project, had sustained winds of >60 mph that lasted, in some areas, up to 36 hrs, and gusts to 95-107 mph. Much of the damage and turbidity was because these high winds lasted much longer than winds from a hurricane do, and the direction from which they came (the southwest). The turbidity had not yet fully settled, when two weeks later another intense storm hit. In Florida Bay, seagrass die-off, which was likely the result of a suite of environmental conditions, initially caused the direct loss of over 4,000 Ha of seagrass, largely *Thalassia* (Robblee et al, 1991). While the initial dieoff has subsided, secondary algal blooms and turbidity plumes are blanketing hundreds of square kilometers, and causing general seagrass losses over wide areas. In Texas, protracted brown tides have for many years now periodically covered seagrass sites. St. Joseph Bay experienced stress in the form of heavy grazing pressure by sea urchins and a major rain event that dropped salinities to 10 ppt and the resulting influx from the watershed produced increased color in the water for a protracted time. These facts show the level of stress to which the communities in the coastal zone are being subjected around the entire periphery of the Gulf of Mexico.

Table 8-1. Comparison of *Thalassia testudinum* parameters at all sites for the summer of 1993. South Florida uses Rabbit Key Basin data.

		Rabbit Key Basin South Florida	Texas	St. Joe Bay Florida
	Latitude	25.0 N.	27.5 N.	29.3 N.
Turnover Rate	%/d	1.6-1.7	2.4-2.8	1.8-3.0
Areal Productivity	g/m2/d	2.5	2.4-3.3	2-3
Leaf Production/shoot	mg/ss/d	2.3-2.8	4.2-4.4	3.4-6.5
Standing Crop	g/m2	146-163	101-123	100-111
Biomass	g/m2	370-417	560-917	450-790
Above/Below Ratio		0.1	0.1-0.15	.16-.28
Shoot Density	ss/m2	880-1080	506-785	490-590
Blade Length	cm	17.0	15-21	24.0
Blade Width	mm	8.0	7.0	11.0
LAI	m2/m2	1.2-1.4	2.4-2.8	.9-1.2

The accompanying tables and figure summarize the findings across all of the field sites. Table 8-1 shows the variation in the parameters of the seagrasses at the three research sites. The numbers represent the conditions from the initial sample through the first summer. While many are given in ranges, they still show some significant differences in the structure at the different sites. Turnover rate had the least variation in south Florida, probably due to its lower seasonal climatic variation, but south Florida had the lowest turnover rate which is unusual as turnover usually increases towards the equator. Areal productivity was quite consistent among the sites. The south Florida site also had the least production per shoot, but areal production remained high as shoot numbers in south Florida were very high. The density of shoots in south Florida was significantly higher than the other sites, and was twice the density at the northern Florida site. Standing Crop was highest in south Florida by 30-50%, and Texas and north Florida were nearly identical. Although standing crop was

highest in south Florida, total biomass was the lowest, with both north Florida and Texas having 50-100% higher total biomass

As a result, the above/below ground ratios were lowest in south Florida with only 10% above ground material. Texas ranged from 10-15% and the north Florida site was 16-28% above ground biomass. Short shoot densities were typically high in south Florida, and were typically about twice the shoot density in north Florida. The densities in Texas were intermediate. The *Thalassia* blades at the north Florida site were very robust. Blade lengths in north Florida were 40% longer than in south Florida and Texas, although Texas showed much more variation. Blade widths in south Florida and Texas were relatively narrow and were nearly 50% greater at the north Florida site. Although the individual leaves were robust in north Florida, they were relatively less abundant than elsewhere, and the LAI for the two Florida sites was just over 1 while the Texas site had LAI's of 2.4 to 2.8.

Table 8-2 shows the very wide variation in light fields found across the region. Fundamentally it shows the propensity for fouling at each of the three localities. In all cases the mesh, mesh size, and cages were identical. The St. Joseph's Bay Florida site was the northern most site, and had the least light reduction effect from the cages . The resulting light levels there were near design levels, and that is reflected in the plant response.

Table 8-2. Incoming Photosynthetically Active Radiation (PAR) delivered to the top of the canopy of the two light reduction treatments as a percentage of the light received at the top of the canopy of the control plots at the three sites.

	Rabbit Key Basin South Florida	Texas	St. Joe Bay Florida
Latitude	25.0 N.	27.5 N.	29.3 N.
Coarse Mesh (3/4 in)	43 % (range 30-49%)	14%	60-70 %
Fine Mesh (1/4 in)	21%	5 %	30-40 %

Both the south Florida and Texas experienced much higher than anticipated levels of fouling. This was so severe at the Texas site that the decrease in light reaching the canopy was about 5 times greater than the decrease in north Florida and over 3 times greater than the south Florida site.

Despite the wide differences in the basic makeup of the seagrass meadows tested, and the generally greater than designed light attenuation, some very consistent patterns emerged from the sites. This response is summarized in figure 8-1. This figure shows the basic patterns of response to light attenuation seen at the three sites. The upper lines from the three site depictions are the control plots. In south Florida and St. Joseph's Bay, there was a slight upward trend in the principal parameters. In general this is within the normal variation found on a site. The Texas site was different. There was a very pronounced downward trend in the data, even at the control plots. This was possibly due to the effects of the chronic brown tides that have plagued that area for several years.

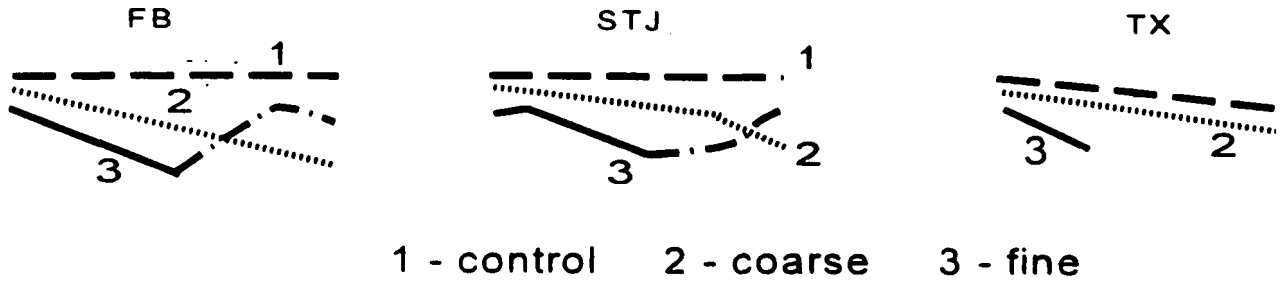


Fig. 8-1. Trends in seagrass responses at the three sites, Florida Bay (FB), St. Joseph's Bay (STJ), and Corpus Christi Bay (TX).

At the coarse mesh treatments, the south Florida site and the Texas site, with their greater light attenuation due to fouling showed pronounced downward trends, as would be expected under those circumstances. By contrast, the north Florida site showed very little response to the decreased light until the second year, at which time the plant parameters began to decline with continued light reduction. For the fine mesh treatments there was also a lag period at the north Florida site, but declining plant performance was detected in the first year. In these treatments, with their high light reduction, the plants declined relatively rapidly. When the fine mesh cages were removed at the end of the first summer, the seagrasses at the Florida sites began a general rebound, but the Texas site was completely destroyed by that time.

These results show that there is no good level of light reduction. With 30% of less attenuation from background the St. Joseph's Bay stations showed a lag before beginning declines, indicating a use of stored reserves to weather a short-term stress. At the stations that suffered severe light reduction, but where seagrasses still survived, there was recovery after the removal of the light reduction stress.

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