

LIGHT REQUIREMENTS OF *Thalassia testudinum* IN TAMPA BAY, FLORIDA

FINAL REPORT

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Surface Water Improvement and Management Program
Southwest Florida Water Management District
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TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGEMENTS	i
TABLE OF CONTENTS	ii
LIST OF FIGURES	v
LIST OF TABLES	xii
EXECUTIVE SUMMARY	xiv
INTRODUCTION AND BACKGROUND	1
PROJECT PLAN	2
METHODS	3
Site Selection	3
Halodule	4
Instrumentation	6
Field Work	7
Instrument Maintenance, Downloading	7
Areal Density	8
Seagrass Growth Measurements	8
Biomass Cores	9
Sediments	9
Laboratory Analyses	9
Above-ground Growth	9
Reconstructive Aging	10
Epiphytic Attenuation	11
Carbohydrates	12
Biomass Cores	12
Sediments	13
Statistical Testing	13
Data from Other Sources	14
Productivity-Irradiance Measurements	14
Water Column Monitoring	14
Solar Irradiance	15
Tidal Data..	15
PAR Data Reduction	17
Bottom Reflectance	21

	Page
RESULTS	24
Data Completeness	24
Light Climate	24
Representativeness of Monitoring Year	24
Net Change in Areal Extent	24
Salinity	27
Temperature	27
Water Clarity	28
Attenuation Coefficient Characteristics	28
Diurnal and Seasonal Patterns	28
Annual Means	30
Comparison between Stations	30
Station Water Depths	30
Percentages of PAR	31
Water Column Characterization of Shallow and Deep Stations	32
Epiphytic Attenuation	32
Total Attenuation	34
Annual Light Regimes	35
Similarity of MML and Other Monitoring Programs	36
Extension of Light Requirements to the Remainder of Tampa Bay	37
<i>Halodule wrightii</i>	39
Seagrass Biomass and Growth Parameters	42
Shoot Density	43
Biomass and Tissue Percentages	44
Mean Blade Length	46
Leaf Area Per Shoot	47
Leaf Area Index	48
Leaf Relative Growth Rate	48
Above-ground Growth	49
Areal Growth	49
Plastochrone Interval	50
Epiphyte Biomass	51
Ratio of Epiphyte to Above-ground Seagrass Biomass	51
Percent Ash Free Epiphyte Biomass	51
Carbohydrates	52
Sediments	53
Photosynthetic Parameters	54
Light Climate	56
Average Daily Total PAR	57

	<u>Page</u>
H_{sat} (Adjusted for Epiphytic Attenuation)	58
$H_{comp-leaf}$ (Adjusted for Epiphytic Attenuation)	58
Interrelationships of Growth and Abiotic Factors	59
SUMMARY	60
LITERATURE CITED	69

Appendix A Seagrass Restoration Targets for Tampa Bay

Appendix B Statistical Results

Appendix C Raw Data

LIST OF FIGURES

- Figure 1. Study location for the determination of light requirements of *Thalassia testudinum* in Tampa Bay.
- Figure 2. Stations locations and designations for continuous light (PAR) monitoring in Tampa Bay.
- Figure 3. Apparatus for continuous monitoring of underwater PAR in Tampa Bay. Vertical separation of sensors is 0.5 m. Lower sensor is oriented toward the south. Approximate station latitudes are 27.5°N.
- Figure 4. Schematic representation of monitoring sites for Thalassia in Tampa Bay. Continuous PAR instrumentation was placed just outside of marked edge at deep station.
- Figure 5. Apparatus for determination of PAR attenuation due to epiphytic material.
- Figure 6. Continuous light monitoring stations and tidal differences available for Tampa Bay.
- Figure 7. Examples of the correspondence of predicted tidal heights with observed initiating data for PIN and RIV.
- Figure 8. Example of the effects of weather on water levels and the resultant overprediction of tidal heights during winter storms with northerly winds.
- Figure 9. Residuals from tidally varying water depth predictions. Upper figure (a) illustrates lack of dependence on rate of change in predicted tide (i.e., no significant phase shifts between observed and predicted data). Lower figure (b) illustrates the weather-induced deviations of observed depths from predicted tides.
- Figure 10. Fouling rates (percent PAR reduction day⁻¹) measured on PAR sensors and used for correction of recorded PAR data.
- Figure 11. Annual patterns of salinity at continuous PAR monitoring stations. Samples were typically surface grabs samples.
- Figure 12. Annual patterns of temperature at continuous PAR monitoring stations. Data illustrated are for MUL.

- Figure 13. Annual average Secchi depths for Hillsborough County Environmental Protection stations in Hillsborough (HB), Middle Tampa (MTB), and Lower Tampa Bays (LTB) (Source: Ring Engineering Asst., 1992).
- Figure 14. Observed water column PAR for top and bottom sensors and calculated attenuation coefficients at the maximum depth limits of *Thalassia* beds during the periods between seagrass blade marking and recovery. Illustrated for the MUL deep station.
- Figure 15. Observed water column PAR for top and bottom sensors and calculated attenuation coefficients at the maximum depth limits of *Thalassia* beds during the periods between seagrass blade marking and recovery. Illustrated for the PIN deep station.
- Figure 16. Observed water column PAR for top and bottom sensors and calculated attenuation coefficients at the maximum depth limits of *Thalassia* beds during the periods between seagrass blade marking and recovery. Illustrated for the PRT deep station.
- Figure 17. Observed water column PAR for top and bottom sensors and calculated attenuation coefficients at the maximum depth limits of *Thalassia* beds during the periods between seagrass blade marking and recovery. Illustrated for the RIV deep station.
- Figure 18. Incident (in air) irradiance (solid line) and wind speed (broken line) at Mote Marine Laboratory (~35 km to the south of Tampa Bay), during the periods between seagrass blade marking and recovery.
- Figure 19. Diurnal variations in attenuation coefficient (diamonds) produced by varying solar elevation. Annual variations in the magnitude of diurnal variation.
- Figure 20. Attenuation coefficients (K_0) determined between 1000-1400 hours at Tampa Bay continuous light stations, monthly means and standard deviations by station.
- Figure 21. Maximum depth limits as a function of water column attenuation (K_0) alone. Comparison of maximum depth limits of seagrass beds in Tampa and Sarasota Bays with the annual average isolume of 22.5% as received by Tampa Bay stations. Sarasota Bay data include data from both *Thalassia* and *Halodule* beds. The effects of epiphytic attenuation are not included.

- Figure 22. Relationship of epiphytic loads, both total and ash-free mgdwt cm^{-2} , with PAR attenuation determined as an integrated whole shoot value.
- Figure 23. Empirical relationship of epiphytic load (mg of ash-free mgdwt cm^{-2}) to integrated whole shoot PAR attenuation.
- Figure 24. Seasonal patterns of epiphytic attenuation at maximum depth limits of *Thalassia* beds in Tampa Bay.
- Figure 25. Epiphytic attenuation of PAR by depth, month, and station for Tampa Bay.
- Figure 26. Seasonal patterns of epiphytic attenuation of PAR by station for Tampa Bay.
- Figure 27. Maximum depth limits of Tampa Bay *Thalassia* stations as a function of attenuation coefficient (K_0). Attenuation coefficients computed from annual averages of percentage PAR remaining in the water column at depth (annual water column K_0 and with the attenuation due to epiphytes included (annual total K) (see text). Isolumes illustrated are average percentages of four stations.
- Figure 28. Annual total attenuation coefficients (water column and epiphytic attenuation combined) and maximum depth limits for Tampa and Sarasota Bay stations. Sarasota Bay data produced from biweekly samplings and include measurements at both *Thalassia* and *Halodule* beds.
- Figure 29. Monthly averages of the total PAR per day received at the maximum depth limits of *Thalassia* beds in Tampa Bay.
- Figure 30. Comparison of monthly mean attenuation coefficients (1000-1400 hours) determined from continuous monitors and measured during monthly interval samplings by Hillsborough County Environmental Protection Commission. Stations compared are the closest available to continuous light sites, although for the RIV site, the nearest HCEPC is some distance away.
- Figure 31. Comparison of monthly mean attenuation coefficients determined by continuous monitoring with the envelope described by the HCEPC stations in lower Middle and Lower Tampa Bay (HCEPC Stations 19,21,23,24, 25, 28, 90, 91, 92, 95 and 96).
- Figure 32. Locations of Hillsborough County (•) and City of Tampa (■) routine water quality monitoring stations.

- Figure 33. Routine monitoring stations. Stations (○) which meet annual average water clarity requirements for *Thalassia* under moderate (38.7 %) epiphytic attenuation, but not under high (50.0%) attenuation. Stations (●) which do not meet requirements under moderate or high epiphytic attenuation.
- Figure 34. Routine monitoring stations. Stations (○) which meet growing season (May-Sept) average water clarity requirements for *Thalassia* under moderate (38.7%) epiphytic attenuation, but not under high (50.0%) attenuation. Stations (●) which do not meet requirements under moderate or high epiphytic attenuation.
- Figure 35. Seasonal patterns of total attenuation (both from water column and epiphytic load) on *Thalassia* and *Halodule* from Sarasota Bay. Samples collected from the maximum depth limits of individual stations and under a variety of nutrient loading conditions (Source: Dixon and Kirkpatrick, 1995).
- Figure 36. *Thalassia* shoot density (shoots m⁻²) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means of approximately 40 quadrat counts.
- Figure 37. *Thalassia* above-ground biomass (gdwt m⁻²) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10.
- Figure 38. *Thalassia* above-ground biomass (gdwt m⁻²). Comparisons among shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10).
- Figure 39. Percent of total *Thalassia* biomass from roots and rhizomes, short shoots, and blades at all stations during December 1994. Ratio of above to below-ground biomass. Values are means ± 1 s.d.; n = 10.
- Figure 40. Percent of total *Thalassia* biomass from roots and rhizomes, short shoots, and blades at all stations during April 1994. Ratio of above to below-ground biomass. Values are means ± 1 s.d.; n = 10.
- Figure 41. Percent of total *Thalassia* biomass from roots and rhizomes, short shoots, and blades at all stations during August 1994. Ratio of above to below-ground biomass. Values are means ± 1 s.d.; n = 10.
- Figure 42. Percent of total *Thalassia* biomass from roots and rhizomes, short shoots, and blades at all stations during October 1994. Ratio of above to below-ground biomass. Values are means ± 1 s.d.; n = 10.

- Figure 43. Mean *Thalassia* blade length (cm shoot^{-1}) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 44. Mean *Thalassia* blade length (cm shoot^{-1}). Comparison among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 45. *Thalassia* leaf area ($\text{cm}^2 \text{ shoot}^{-1}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 46. *Thalassia* leaf area ($\text{cm}^2 \text{ shoot}^{-1}$). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 47. *Thalassia* leaf area index ($\text{m}^2 \text{ m}^{-2}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 48. *Thalassia* leaf area index ($\text{m}^2 \text{ m}^{-2}$). Comparisons among shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 49. *Thalassia* leaf relative growth rate ($\text{mgdwt gdwt}^{-1} \text{ day}^{-1}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 50. *Thalassia* leaf relative growth rate ($\text{mgdwt gdwt}^{-1} \text{ day}^{-1}$). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 51. *Thalassia* blade production ($\text{mgdwt shoot}^{-1} \text{ day}^{-1}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 52. *Thalassia* blade production ($\text{mgdwt shoot-1 day-1}$). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 53. *Thalassia* areal growth ($\text{gdwt m}^{-2} \text{ day}^{-1}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).

- Figure 54. *Thalassia* areal growth ($\text{gdwt m}^{-2} \text{ day}^{-1}$). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15).
- Figure 55. Median turnover time of *Thalassia* at shallow and deep stations for each of four sites from December 1993 through October 1994.
- Figure 56. Median turnover time of *Thalassia*. Comparison among both shallow and deep stations at all sites from December 1993 through October 1994.
- Figure 57. Ratio of epiphyte biomass to above-ground *Thalassia* biomass (blade weights) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10).
- Figure 58. Ratio of epiphyte biomass to above-ground *Thalassia* biomass. Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10).
- Figure 59. Ash-free epiphyte biomass as a percent of total epiphyte biomass at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10).
- Figure 60. Ash-free epiphyte biomass as a percent of total epiphyte biomass. Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10).
- Figure 61. *Thalassia* rhizome soluble carbohydrate levels (mg gdwt^{-1}) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10).
- Figure 62. *Thalassia* rhizome soluble carbohydrate levels (mg gdwt^{-1}). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d. ; n = 10).
- Figure 63. Sediment parameters at shallow and deep stations for each of four sites from January 1994. Values are means ± 1 s.d.; n = 5).
- Figure 64. Average daily total PAR ($\text{E m}^{-2} \text{ day}^{-1}$) for the two week period prior to *Thalassia* productivity measurements at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.

Figure 65. Average daily total PAR ($E\ m^{-2}\ day^{-1}$) for the two week period prior to *Thalassia* productivity measurements. Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.

Figure 66. H_{sat} , average number of hours per day that PAR ($\mu E\ m^{-2}\ sec^{-1}$) was equal to or greater than saturating irradiance (E_k) at shallow and deep stations for each of four sites from December 1993 through October 1994. PAR levels adjusted for epiphyte attenuation. Values are means ± 1 s. d.

Figure 67. H_{sat} , average number of hours per day that PAR ($\mu E\ m^{-2}\ sec^{-1}$) was equal to or greater than saturating irradiance (E_k). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. PAR levels adjusted for epiphyte attenuation. Values are means ± 1 s.d.

Figure 68. $H_{comp-leaf}$ average number of hours per day that PAR ($\mu E\ m^{-2}\ sec^{-1}$) was equal to or greater than compensation irradiance for leaf tissue (E_{c-leaf}). at shallow and deep stations for each of four sites from December 1993 through October 1994. PAR levels adjusted for epiphyte attenuation. Values are means ± 1 s.d.

Figure 69. $H_{comp-leaf}$ average number of hours per day that PAR ($\mu E\ m^{-2}\ sec^{-1}$) was equal to or greater than compensation irradiance for leaf tissue (E_{c-leaf}). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. PAR levels adjusted for epiphyte attenuation. Values are means ± 1 s.d.

LIST OF TABLES

- Table 1. Dates of *Thalassia* blade punching and retrieval at stations in Tampa Bay. Biomass cores collected when marked shoots recovered. Samplings referred to in text as December, February, April, June, August and October (consistent with marking dates) to emphasize bimonthly nature of sampling.
- Table 2. Time periods of missing continuous light data.
- Table 3. Annual mean Secchi depth for individual HCEPC stations, 1994.
- Table 4. Water column attenuation coefficients measured at the maximum depth limits of *Thalassia* between 1000-1400 hours.
- Table 5. Mean water depths and approximate elevations of the maximum depth limits of *Thalassia*.
- Table 6. Percentage of PAR at the maximum depth limits of *Thalassia* from data collected between 1000-1400 hours. Computed with fixed and tidally varying station depths.
- Table 7. Epiphytic attenuation of PAR due to epiphytic load measured on individual shoots of *Thalassia*. Units are % attenuation.
- Table 8. Percentage of PAR available to *Thalassia* at maximum depth limits computed from water column attenuation coefficients and epiphytic attenuation, fixed water volume depths and data collected between 1000-1400 hours.
- Table 9. Absolute PAR levels recorded *Thalassia* at maximum depth limits. Monthly values of maximum observed PAR, average PAR (during daylight hours), and average daily total PAR.
- Table 10. Absolute PAR levels recorded at *Thalassia* maximum depths limits after water column and epiphytic attenuation. Monthly values of maximum observed PAR, average PAR (during daylight hours), and average daily total PAR.
- Table 11. Annual totals of PAR both in the water column and received by *Thalassia* (after epiphytic attenuation) at maximum depth limits in Tampa Bay.

- Table 12. Seasonal and station means of epiphytic attenuation of PAR measured at stations in Sarasota Bay (n = 5 for each station-date).
- Table 13. Mean percentage of PAR at target depths of 1.34 m, 1.84 m, 1.84 m, and 2.34 m for HB, respectively (1.0 m, 1.5 m, 1.5 m, 2.0 m mllw). Annual water column requirement of 22.5 % based on plant requirement of 13.8 % annually, and mean epiphyte attenuation of 38.7% for the year. Final column assumes a calculated water column requirement of 27.5 % based on 13.8 % annual plant requirement and annual epiphytic attenuation of 50%.
- Table 14. Mean percentage of PAR at target depths of 1.34 m, 1.84 m, 1.84 m, and 2.34 m for HB respectively (1.0 m, 1.5 m, 1.5 m, 2.0 m mllw). Water column requirement during the growing season 16.1% based on plant requirement of 12.0 % and mean seasonal epiphyte attenuation of 25.5 %. Final column assumes a calculated water column requirement of 21.4 % based on 12.0% seasonal plant requirement and growing season epiphytic attenuation of 43.9 %.
- Table 15. Plastochrone interval (days) and approximate numbers of blades per shoot per year produced by *Thalassia* in Tampa Bay.
- Table 16. Photosynthesis/irradiance parameters determined on *Thalassia* leaf segments from Tampa Bay during April and June. Units are ($\mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1}$) ($\mu\text{E m}^{-2} \text{ sec}^{-1}$) $^{-1}$; E_C and E_k , $\mu\text{E m}^{-2} \text{ sec}^{-1}$; P_{max} , $\mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1}$; chlorophyll a and b, mg gdwt^{-1} (Data from Dr. C.J. Dawes)

EXECUTIVE SUMMARY

The Water Quality Assessment Project, sponsored by the Surface Water Improvement and Management Program (SWIM) of the Southwest Florida Water Management District (SWFWMD), was developed to determine the light requirements of *Thalassia testudinum* within Tampa Bay. The project was one of several conceived to form a causal chain linking watershed management and loadings control with water quality (chlorophyll and solids), light attenuation, and seagrass cover within the Bay.

The project collected a continuous record of in situ light climate data (scalar attenuation coefficients of photosynthetically active radiation [PAR]) for more than a calendar year at four locations in Tampa Bay. Stations were selected at the deep, light-limited edges of *Thalassia* meadows. Attenuation of light by the epiphytic material on seagrass blades was also measured. In addition to light measurements, biomass, above-ground growth, and condition measurements were performed quarterly or bimonthly at both the maximum depth extent of the seagrass beds and at shallower (non-light-limited) locations. The light requirements so determined were evaluated against average light attenuation data provided by other monitoring projects and against seagrass target depths for other portions of Tampa Bay.

Seasonal patterns in biomass and condition of *Thalassia* were quite evident and generally exceeded any station-to-station differences, but the deepest station in the study exhibited evidence of morphological adaptations to lowered light levels. Adaptations primarily consisted of increased blade lengths, decrease in blade production per year, and a much higher ratio of above to below ground biomass. Other indications of stress were a significant reduction in shoot density in contrast to expected seasonal patterns.

With the knowledge that PAR at one of the deep stations may be at unacceptable levels, or at a minimum that morphological adaptations to shading were triggered, the light climate may be examined knowing that the data encompass a threshold value. Water clarity for Tampa Bay during the project year was comparable to longer term values (approximately 1985-1990), except in Hillsborough Bay, where a continued improvement in water clarity conditions was observed. With Lower Tampa Bay water clarity during the project year comparable to previous conditions, grassbeds can be presumed to be at a steady state with respect to light.

Annual percentages of light present in the water column at the maximum depth limits of *Thalassia* averaged 22.5% of subsurface scalar irradiance. Percentages represent attenuation by materials in the water column only and can be transferred to other areas as appropriate management targets only if epiphytic growth is comparable. Light percentages received during the growing season were somewhat less, and reflect typical decreases in water clarity observed during the summer wet season. Seasonal patterns of both light and growth emphasize the fact that the two parameters are

temporally decoupled, the storage of *Thalassia* rhizomes permitting an integration of any adverse conditions over a longer time period.

Annual averages of light actually available to the *Thalassia* blades (adjusted for both water column and epiphytic attenuation) were between 13.9 % and 14.2 % of subsurface irradiance for the three sites where seagrass condition appeared acceptable, while the station with the shade adapted *Thalassia* received 13.0 %. **The percentage of light remaining after total attenuation by both water column and epiphytes (13-14%) is not an appropriate management target for water column clarity alone, unless epiphytes on *Thalassia* are completely absent.**

The extrapolation of measured PAR climates to *Halodule* was difficult due to the absence of clearly depth- or light-limited beds near the study sites. Although there are incidental reports of *Halodule* occurring at greater depths than *Thalassia*, and Sarasota Bay data indicate that *Halodule* can withstand periods of much lower irradiance, literature reports of annual light climates (in Sarasota Bay and Texas) and critical light values (in Florida Bay) indicate *Halodule* may have annual light requirements roughly equivalent to or slightly greater than *Thalassia*.

Station depths (seagrass depth limits) ranged between 1.63 and 2.01 m mean lower low water (MLLW), with standard errors of each station depth near 0.02 m. *Thalassia* at the deepest station exhibited shading responses with an unknown outcome. The remaining stations ranged between 1.63 and 1.81 m MLLW. The maximum depths of the various stations each received approximately 22.5% of subsurface PAR. Water clarity was presently insufficient to permit penetration of 22.5 % PAR (or seagrass growth) to the 2.0 m depth recommended for Lower Tampa Bay. (Recommended or target restoration depths by Bay segment were conservatively selected to include approximately 95 % of the observed maximum depths of seagrasses identified in 1950 and to allow restoration of grasses to 1950 acreages.)

As water clarity in Lower Tampa Bay has been relatively stable over the last number of years, seagrass maximum depths at three of the four stations are not expected to increase substantially, and maintaining present water clarity is not expected to result in expansion to 2.0 m MLLW depths at these locations. It is unknown whether the target depth can be maintained at the one station evidencing shade adaptations.

The areal extent (and, presumably, depths, as well) of seagrasses at the four stations monitored, however, may already be comparable to the target 1950's areal distributions. The stations were located in areas with relatively small historical losses at the deep edges of the seagrass beds. The level of resolution of seagrass mapping (± 25 m) will not allow the a more precise determination of whether the present day areal extent (and therefore depth) of seagrasses at the stations Lower Tampa Bay is comparable to the 1950's benchmark within the level of resolution needed by the present study.

Accurate extrapolation of light requirements determined for *Thalassia* in Lower Tampa Bay to other regions of the Bay will depend on the accuracy of assumptions about epiphytic loads in the higher nutrient environments of the upper Bay, and how representative water clarity at deep water stations is of the nearshore environment. Stations which presently fail to meet the best estimates of water clarity requirements are near areas which have suffered the largest historical losses of seagrasses at the deeper edges. As water clarity for most of the Bay (excepting Hillsborough Bay) has been relatively stable since approximately 1985, further increases (from present conditions) in the maximum depth limits of seagrasses are not expected if water clarity (and epiphytic attenuation) remain comparable to present values. The probable lack of depth extensions from present coverages is not directly related to the losses and documented recoveries of seagrass coverages which have occurred in shallower, non-light-limited areas.

In Hillsborough Bay, however, water clarity during 1994 was better than during the 1985-1990 period and areal increases in grasses has been reported. Updated mapping efforts underway at this time will permit a reassessment of seagrass coverage with respect to water clarity, 1950's seagrass coverage, and target depths for this Bay region.

INTRODUCTION AND BACKGROUND

The Water Quality Assessment Project, sponsored by the Surface Water Improvement and Management Program (SWIM) of the Southwest Florida Water Management District (SWFWMD), was developed to answer crucial questions regarding the light requirements of *Thalassia* within Tampa Bay (Figure 1). The project was designed to provide a scientific basis for the resource-based management of keystone species for the Bay system and was one of several projects conceived to form a causal chain linking watershed management and loadings control with water quality (chlorophyll and solids), light attenuation, and seagrass cover within the Bay. Project design was an interactive process between the Seagrass Focus Group comprised of local researchers and agency personnel experienced with seagrass habitats, physiology, distribution, and issues, SWFWMD-SWIM, Mote Marine Laboratory (MML), and the Virginia Institute of Marine Sciences.

PROJECT PLAN

The project was to determine the light climate over a calendar year at the deep edges of *Thalassia testudinum* meadows at four locations in Tampa Bay. At each site, measurements of photosynthetically active radiation (PAR) were to be recorded every 15 minutes at two depths within the water column, such that water column attenuation coefficients could be calculated. These data were to be coupled with measurements of above-ground growth (through leaf punching), and the light requirements so determined were to be evaluated against existing average light attenuation data and seagrass target depths for other portions of Tampa Bay.

Quarterly, biomass (both above- and below-ground) and above-ground growth parameters were quantified at both deep and shallow stations at each of four sites. Attenuation of PAR by the epiphytic material on selected seagrass blades was also measured. Additional support from the SWFWMD, Florida Department of Environmental Protection, Marine Research Institute, and the Sarasota Bay National Estuary Program permitted two additional determinations of above-ground growth and epiphytic attenuation during the project year, resulting in roughly bi-monthly samplings for growth and epiphytic attenuation. Support from the University of South Florida also provided photosynthesis-irradiance data to the project.

Growth was to be examined as a function of light received during the preceding period and light climates were to be interpreted with respect to changes in grassbed coverage during the study year. The observed light climate was to be used to set management goals for water clarity in Tampa Bay by identifying the clarity which will permit seagrass expansion to a selected depth.

METHODS

Site Selection

The goal in site selection was to identify stable grassbeds for instrument deployment and determination of annual light regimes. One site was to be in the lower Bay where conditions were believed to be optimum for *Thalassia*, where extensive meadows of this grass were present, and where the deep edge of the *Thalassia* bed in this area had previously been identified to be light-limited (Hall et al., 1991). The remaining three stations were to be established along a potential nutrient and/or salinity gradient as far up the Bay as suitable sites could be found.

Seagrass coverage trend analysis performed by SWIM narrowed the area for site selection by identifying grassbeds with stable or expanding cover. Potential stands of *Thalassia* were selected both from local knowledge, species transect information available from the SWIM Program (September 1991 and October 1992 sampling), and the photographic signature apparent in the 1990 imagery used for the SWIM change analysis.

Reconnaissance surveys were conducted on the western side of the Bay from north of the Gandy Bridge to Mullet Key. On the eastern shore, investigations were conducted from the Big Bend area (just south of Apollo Beach) south the Manatee River and Anna Maria. All of the SWIM transects in which *Thalassia* appeared at the deep edge were inspected, as well as the areas which appeared to be *Thalassia* in the 1990 photography.

Sites were rejected if an offshore unvegetated sandbar occurred at a shallower depth than the deepest grasses, as this implied that wave action or other physical factors limited SAV expansion and that the deepest occurrence was not necessarily light-limited. Sites were also rejected if the deep edge of a *Thalassia* bed occurred at such a shallow depth that PAR sensors could not be deployed with a minimum 0.5 m separation without frequent exposure (and erroneous data) or without danger to boating traffic.

In some areas with *Thalassia* at the deepest edge, *Thalassia* appeared to be an very minor member of the SAV community and finding enough material to sample throughout the project year would be problematic. It was also necessary that *Thalassia* be the dominant species at the deep edge of an individual bed, as otherwise, competitive advantage of other species rather than available light levels may be the limiting factor to expansion.

Final site selection included four locations (Figure 2),

MUL 27°38.3' 82°41.4' Immediately to the east of Mullet and Conception Keys,

PIN 27°41.8' 82°38.5' To the south of Point Pinellas

PRT 27°37.5' 82°35.0' To the south of the spoil island at Port Manatee, and

RIV 27°31.8' 82°40.1' At the mouth of the Manatee River, on the southern bank.

The deep stations selected were on the edges of the deepest patch beds that could be found at a site and that were large enough (approximately 20 m in diameter) to sustain sampling over the course of the project. (At the selected sites, no deeper patches of any size were observed.) From the deep edge determined at each site, a transect was run normal to bathymetric contours (generally toward shore) until depths were 0.9 m shallower. The shallow site was established at this location. Stations were designated as 'S' (shallow) or 'D' (deep). Both shallow and deep stations were marked with crab trap buoys and trailer tiedowns, with more buoys placed at the deep stations to discourage boat traffic in the vicinity of the instruments.

Shallow sites, with the exception of MUL, were 200-500 m shoreward from the deep sites, with frequent intervening areas of bare sand. This configuration reduces the likelihood of any physiological support for the deeper patch beds from the non-light-limited shallow stations. At MUL, the bottom slope is more acute, and the shallow station is approximately 30 m from the deep station. Grasses are continuous between shallow and deep stations at this site.

Halodule

As budgetary constraints prevented establishing additional continuous light monitoring instrumentation or performing analyses of biomass and growth at sites specific for *Halodule wrightii*, light climates at instrumented sites were to be extrapolated to nearby *Halodule* beds, after compensating for any difference in depths.

Although there are reports of the maximum depth limits of *Halodule* exceeding that of *Thalassia* where the species co-occur (Wigington, 1978; Iverson and Bittaker, 1986; Zieman, 1982; and Tomasko et al., 1993), the patterns of species occurrence in Tampa Bay (Phillips, 1960, 1962; Lewis et al., 1985) indicate that *Halodule* does not typically exist as the deepest seagrass species. Summarized in Lewis et al. (1985), observations indicate that *Halodule* is the most prevalent species in the intertidal zone due to its thermal and salinity tolerance and ability to withstand exposure. *Halodule* can also dominate in the subtidal regions of more turbid areas where other species are absent, implying that a competitive disadvantage (rather than light limitation) may limit its subtidal appearance in other regions of the Bay. Regardless of reported depths, however, inter-annual variations in water quality, varying epiphyte loads and attenuations, the varying storage capability between species, and the colonizing properties of *Halodule* further complicate deduction of light requirements from incidental reports of maximum depth limits.

Inter-species competition investigation by Bloom (1987) demonstrated that *Halodule* transplants into a *Thalassia* bed did not persist unless their root systems were protected from invasion by the neighboring *Thalassia*. Differing sediments in the nearshore environment may also play a role in species distribution, although the literature are divided on whether oxidized (Phillips, 1960) or reducing (Pulich, 1985) sediments are more preferable.

In contrast, a study in which numerical light requirements (compensation and saturation irradiances, E_c and E_k) were quantified for both species indicated that PAR requirements for *Halodule* are **higher** than for *Thalassia* (Fourqurean and Zieman, 1991b). Collection depths of tissue samples were not specified, however, and the plants may or may not have been light limited.

Other work indicates that there may be little difference between the light requirements of the two species. Intensive monitoring of water clarity (Dixon and Kirkpatrick, 1994), demonstrated little difference in annual light regimes, once epiphyte attenuation was accounted for, between the maximum depths limits of relatively monospecific *Thalassia* or *Halodule* beds. Substantial differences were noted, however, between seasonal amounts of PAR received, and it was apparent that *Halodule* could persist through periods of extremely low PAR levels, even though annual totals were comparable.

In short, the reasons for the relative distribution of *Halodule* and *Thalassia* may be either physiological (light requirements, sediments, and the like) or may reflect more subtle competitive disadvantages on the part of *Halodule*. Based on the previously reported distributions in Tampa Bay, it was expected that *Halodule* would be present at depths somewhat less than the selected *Thalassia* stations.

The extension of measured light climates to nearby *Halodule* beds and depths will require that the *Halodule* bed be monospecific to preclude competition, and that the species exists at the deepest edge, i.e., no hinderance to expansion along a depth gradient. In addition, the bed must be close enough to the continuous light station such that using the continuous light data is appropriate. Another major assumption implicit in the approach are that any seasonal differences in light availability affect both *Thalassia* and *Halodule* equally.

In short, no locations fulfilling these criteria were found. Reconnaissance by MML during the site selection, did not record any *Halodule* beds at depth in the vicinity of the eventual four sites. While isolated plants of *Halodule* occurred in six of the eight monitored *Thalassia* beds throughout the study (and most frequently at the shallow PIN station), no apparently depth-limited beds of *Halodule* were found during the establishment of the sites or during the underwater surveys conducted at each location. Isolated plants were recovered in core samples from the deep stations of PIN, PRT, and RIV on a few occasions. Monospecific *Halodule* beds were only observed as shallow fringing beds near the intertidal zone. Surveys did not extend great distances from

(> 0.5 km) from the monitored site due to the uncertainty in extrapolation of attenuation coefficients to other locations. Reference to the SWIM 1991 and 1992 transect data confirmed these observations and indicated that *Halodule* was not present at the deep edges of any areas near the continuous light stations, but was again an intertidal and shallow subtidal species.

While *Halodule* is returning to Hillsborough Bay (Avery, 1991), the patchy coverage generally exists in broad areas of shallows, where determination of depth limitation (as opposed to wave action, for example) is difficult. The elevations of the few apparently depth limited beds on spoil islands in the Bay are unknown at this time (R. Johannson, personal communication).

In view of the absence of *Halodule* beds near continuous light monitors from which to deduce light requirements, and lack of information about current depths to which *Halodule* extends in mono-specific stands, light requirements for *Halodule* are discussed in terms of available literature based on work from the Florida Keys and Texas. Where possible, this information is extrapolated to the extensive data available for water clarity and PAR attenuation in Hillsborough Bay (City of Tampa, Hillsborough County Environmental Protection Commission Monitoring Programs, ongoing).

Instrumentation

Continuous *in situ* irradiance sensors were installed just outside the deep edge of the grassbed at each of four sites. Two scalar (4π) quantum sensors (LI-COR 193SA) were secured to a frame attached to a supporting rod which was firmly imbedded in the sediment (Figure 3). Water depths were such that the sensors were expected to remained immersed at all times. The lower of the two submersible sensors was located at approximately the canopy height (0.2 m above the bottom) to avoid trapping of drift algae and sediment resuspension during periods of high wave energy. The upper sensor was located 0.5 m above the lower sensor. At one location (RIV) where the sensor frame was perpendicular to the prevailing current, a “fence” of polyethylene matting was installed on the bottom and approximately 1 m from the support rod to deflect drift algae and prevent it from catching on the sensors.

The sensor array at each site was oriented facing south and the upper sensor offset from the lower such that maximum solar declination (23.5°) would not produce self-shading errors. Sensors were covered with a single thickness of clear plastic food wrap (secured with rubber bands), to enable fouling communities to be completely removed during each field visit by replacing the plastic wrap. The data logger (LI-COR LI-1000) was contained in a waterproof instrument housing and secured in a submerged PVC and cement instrument shelter nearby. Data logger housings were fitted with zines to reduce corrosion of the securing clamps and both housing and excess cable wrapped in garbage bags to reduce fouling. Thermographs (Ryan TempMentor) were also deployed in the

instrument shelter for a continuous record of temperature (± 0.1 °C) experienced by the site.

Loggers were programmed to store 15 minute average readings every 15 minutes, provided PAR levels were above a threshold of $0.5 \mu\text{E m}^{-2} \text{ sec}^{-1}$. Instrument arrays were operated from November 30, 1993 (MUL), December 1, 1993 (PRT), and December 3, 1993 (PIN and RIV) through December 7, 1994.

Field Work

At each station, approximately 15 m of the deepest edge of the *Thalassia* bed was delineated at the beginning of fieldwork with a combination of cement blocks and metal anchors. The shallow depth was similarly marked with permanent blocks. Prior to each field effort, a line was run, connecting the permanent blocks, such that the areas worked were reproducibly sampled over the course of the study. At the deep stations, cores, quadrat counts, and growth measurements were performed 1.0 meter toward shore from the line to avoid eroding the deep edge during the course of the project. At the shallow stations, measurements were made as close the marking line as practicable. The sampling areas are illustrated schematically in Figure 4.

Instrument Maintenance, Downloading

Sensors and data loggers were retrieved to the boat every two weeks and data downloaded to a portable computer. Sites were visited, however, on average every five days. Initially, during the winter months, visits were scheduled weekly. With warming waters and an increase in fouling, maintenance frequency was increased to every 3-5 days. On each visit, submerged sensors were checked for damage and the protective clear plastic wrap which prevented permanent adhesion of fouling organisms was removed and replaced.

During each visit to the sites, manual PAR profile measurements were made with a portable photometer (LI-COR LI-1000) and PAR sensors (LI-COR 193S [4π] and 190SA [air, 2π]) both adjacent to the fixed submerged sensors and at the shallower stations to determine similarity of light regimes between shallow and deep sites. On multiple occasions, the manual profiles included additional submerged sensors (LI-COR 192SA [2π]) in both upward and downward facing orientations to determine the degree of upwelling light due to bottom reflectance. Other field activities included the collection of samples for salinity (conductivity) and measurement of water depth at the sensor location. Salinities were calculated from conductivity data by the equations of Jaeger (1973).

Data recorded on site included wind direction and velocity, time of retrieval and deployment or of cleaning of the sensors, serial numbers of instruments retrieved and deployed, comments on degree of fouling noted on both top and bottom sensors and

whether fouling was similar on both sensors. When data loggers were retrieved and downloaded, attenuation due to sensor fouling was measured in air and files were examined before replacing the logger and sensors to ensure that the instrumentation was working properly. If sensors were replaced, the sensor-specific calibration factor was entered into the data logger for accurate scaling of recorded data.

Areal Density

Quadrat counts of *Thalassia* shoot density were made bimonthly, during each of the six determinations of growth, along the 15 m work line of both shallow and deep stations. Quadrats were 25 cm x 25 cm (0.0625 m²) and approximately 40 were counted for each station and date.

Seagrass Growth Measurements

Measurements of above-ground growth rates were made on six occasions throughout the project year using the blade marking techniques after Tomasko and Dawes (1989). For *Thalassia*, new blades arise from the interior of the leaf bundle and the growth measurement technique assumed the elongation of the outer or oldest blades to be negligible. A needle inserted through the leaf bundle at the base of the blades resulted in a punch mark on the individual blades being displaced upwards with, and proportional to, growth. If the youngest blade contained no punch mark, then it was assumed to have been formed since the bundle was punched. Blade bundles were punched and then recovered after a period (7-14 days) was allowed for growth. On collection, the entire shoot was severed at the level of the punch mark on the oldest blade, and all tissue between the severed base and the punch mark of each blade was assumed to represent new growth. The new tissue formed quantified above-ground growth, since below-ground growth is not measured and total production during any one period may be underestimated.

At each selected depth, 30 individual shoots were marked by punching a syringe needle (20 or 21 gauge) through the entire leaf bundle 1 cm above the blade sheath boundary of the oldest blade. The mark was placed to one side of the midline of the blade to avoid interference with vascular systems and blade necrosis. Marked shoots were tagged with nylon cable ties and short lengths of plastic surveying tape to aid in retrieval. Cable ties were gently tightened to avoid constricting the blade bundle.

Periods of time between tagging and recollection were determined by reference to nearby seasonal data from Sarasota Bay (D. Tomasko, personal communication), and ranged between 10-21 days for winter months and 6-7 days during periods of expected peak growth. Tagging and retrieval dates are listed in Table 1. Where marking and recovery took place in different months, samplings of both growth and biomass are referred to by the month of tagging to emphasize that samplings were roughly bi-monthly in nature. All shoots tagged (which could be found) were recovered, although only 15 were

scheduled for processing from each station on each date. Storm events removed tags on several occasions, resulting in recovery of less than 15 shoots.

During collection of shoots, a long-bladed knife was used to sever the rhizomes on each side of the shoot, and a section of the associated rhizome (4-5 cm) was collected for shoot-specific measurements of rhizome carbohydrate content on up to ten samples per station. Shoots and associated rhizome tissues were individually bagged and held in the dark in insulated coolers at ambient temperatures while in the field and in the dark at 4°C on return to the laboratory.

Biomass Cores

Cores were collected on four occasions during the sampling year, during early January, early May, late June, and late October-early November samplings. A 12.5 cm x 12.5 cm (0.0156 m²) diver operated corer was used to collect above-and below-ground biomass to a depth of approximately 20 cm. Care was taken to include only the above-ground biomass which originated within the core area. A knife was used to assist in core penetration, if necessary, and to excavate the resulting core with minimal loss of rhizome tissue. Cores were transported to the boat while in the coring device and sieved of excess sediments before bagging individually. Care was also taken to avoid detaching shoots from any associated rhizomes. Core samples were held in insulated coolers at ambient temperatures while in the field and at 4°C on return to the laboratory.

Sediments

Sediment samples were collected during early January at all sites for the determination of grain size and percent organic content. Diver-operated push cores (PVC, 3.8 cm x 15.2 cm, with end caps) were used to collect surficial sediments (5 samples) at both shallow and deep stations of all sites for a total of 40 samples. Sediments were frozen until analysis.

Laboratory Analyses

Above-ground Growth

Of the 30 marked *Thalassia* shoots per station and date, 15 were processed for above-ground growth determinations. A total of only 696 samples were processed due to the losses of some markers during storm events. Apical shoots were avoided. Processing consisted of gently rinsing with deionized water to remove sediment and unattached materials. Necrotic tissue (black or brown, with no apparent green portions) was dissected and removed, as was the marking tag. The blades were separated from the shoot at the original punch mark on the oldest blade, perpendicular to the axis of the blade. Measurements recorded on the productive portion included the number of blades, individual blade widths of up to five blades, and lengths of all blades.

Major taxa of epiphytes were identified, and the blades gently scraped of all epiphytic material (both epiphytes and epifaunal) with razor blades, maintaining as much of the original epiphyte structure as possible. The suspension of epiphytic material was transferred to a jar for later attenuation measurements and load determinations.

The cleaned blades were separated into old and new tissue at the punch mark on each blade and the appearance of any new blades noted. The two tissues were dried in tared foil to a constant weight at 103-105°C. Weights were recorded to 0.0001 g. Calculations included determination of above-ground biomass, leaf-, shoot-, and area-based growth rates, leaf areas, and turnover times. Plastochrone interval for each site was calculated as the time interval between marking and collection, divided by the fraction of blades with new leaves (with no punch marks) appearing (Brouns, 1985). Measurements were transformed from shoot-based to standard areal units (per m²) based on quadrat counts (25 cm x 25 cm, n ~40) of short shoot densities at each site.

Reconstructive Aging

Reconstructive aging analysis (in which the age of individual shoots is determined from either measured plastochrone interval or frequency distribution of the number of leaf scars per shoot) was performed for information on population status. Methods were drawn from Gallegos *et al.*, 1992, 1993; Duarte *et al.*, in press; Durako, in review), as summarized by Durako (unpublished data). Intact (attached to the rhizome) short shoots were cleaned of leaf detritus and the leaf scars girdling the shoot enumerated under approximately 10X magnification. Since shoots were collected at different times, plastochrone intervals (days between initiation of successive blade production) were used to normalize all shoots to the final October sampling.

For normalization, plastochrone intervals at each station were assumed to be in effect from the time of determination, until the next subsequent determination. Growth measurements were performed approximately every two months. The number of blades produced in the roughly 60 day period was calculated as the time interval (in days), divided by the plastochrone interval (in days per blade). The number of blades estimated to have been produced during each successive period was added to the original number counted on the short shoot. The shoots punched in December, for example were augmented by the blades produced during the five succeeding growth periods. The number of leaf scars on shoots collected in October were used directly, with no adjustment.

Data from a single station were normalized and pooled and a frequency analysis performed. From the histogram, the scar classes with comparatively more observations were used to identify annual cohorts (Duarte and Sand-Jensen, 1990). The mean annual production (in terms of numbers of blades) were calculated by difference between the classes of the cohorts, and the average annual production of blades per year used to compute the decimal age of individual shoots. Calculated ages were underestimates, as

the existing blades on the shoots were not included in the total of leaf scars. A second histogram of the aged shoots was prepared using years as classes, and an exponential curve (below) fit through regression,

$$N(t) = N(0) \cdot e^{-Mt}$$

where $N(t)$ is the number of shoots at time (t) , $N(0)$ is the number of shoots at time $= 0$, m is the instantaneous mortality rate in $\ln(\# \text{shoots})$ per year, and half-life, in years, is $T_{1/2} = \ln(2) / m$. Gross shoot recruitment is computed as the proportion of shoots less than a year old, and net annual shoot production determined as the difference between gross shoot recruitment and mortality.

Results of the analysis must be considered to be approximate due to the assumptions involved in normalization of all shoots to a single time, and as the number of shoots available for the calculation were substantially less than the 200 recommended (Durako, unpublished data). Shoot densities would have necessitated the removal of approximately $10-15 \text{ m}^2$ of biomass at each deep station, approximately 2 m^2 at all shallow stations, and concern over this level of destructive sampling restricted the use of this technique.

Epiphytic Attenuation

Determination of PAR attenuation due to epiphytic materials (epiphytes, attached epifauna, sediment, and detritus), dry weights, and ash-free dry weights were determined on ten of the 15 shoots per station used for bi-monthly growth determinations. As only the light attenuating properties of the epiphytic community was investigated during the project, no separation or distinction was made between epiphytes and epifauna, and the term epiphytes and epiphytic materials refers to all materials and organisms which were scraped from the *Thalassia* blades. A total of 478 samples were processed.

Each sample consisted of a single shoot, with the obviously necrotic portions (blackened or brown tissue, with no visually apparent chlorophyll), and associated epiphytic material, removed and discarded. Laboratory processing consisted of gentle scraping of epiphytes, epifauna, and attached detritus (referred to collectively as epiphytes or epiphytic material) from both sides of the productive portions of the seagrass blades (non-necrotic blades above the blade-sheath boundary) with razor blades. The structure of any epiphytic material (such as bryozoans) was retained as much as possible. Total blade area scraped (lengths 1 average width 1 2) was also determined.

Epiphytic attenuation was determined by the method of Dixon and Kirkpatrick (1995), with the apparatus illustrated in Figure 5. The suspension of scraped material was placed into a transparent (acrylic) dish, 71.3 cm^2 in area. The area of the dish was selected based on the total surface area (2 1 blade area) of a “typical” shoot, empirically determined. The walls of the transparent dish were lined with reflective mylar, and the dish illuminated with a quartz-halogen light source (Dyna-Lume 240-350) and a white

acrylic diffusing slide. A cosine PAR sensor (LI-COR 190SB) was placed 12 cm below the dish with epiphytes in the center of a column of the same size as the dish. The sensor tube was also lined with reflective mylar. For each sample, a blank reading of the irradiance passing through an equivalent depth of deionized water was determined, followed by three successive readings of the irradiance penetrating the epiphyte suspension. The suspension was manually stirred and irradiance allowed to stabilize between each reading. Sample volumes (and therefore water depths) were held constant.

The inverse logarithmic relationship between the epiphyte suspension density and transmitted irradiance was used to correct for inequalities between dish area and blade area scraped. Analogous variables to epiphyte suspension density could also be blade area scraped (assuming a homogenous distribution of epiphytes over all leaf surfaces), or dish area in which a fixed amount of epiphytes were measured. The line established by the irradiance of the blank (dish area = 0) and the mean irradiance of the sample (dish area = 20.3 or 71.3 cm²) was used to compute the irradiance which would have been measured had the dish area equalled the area scraped (*i.e.*, epiphytic density in dish equivalent to average *in situ* conditions). The blank and corrected irradiance were then used to compute a corrected attenuation. Attenuations so determined are reported in percent, and represent **area-averaged** conditions, *i.e.*, as if the entire epiphyte burden of the productive blades is evenly distributed across both sides of the blade surfaces, old and new tissue alike. Data from individual shoots were paired with individual shoot growth and biomass parameters, but were averaged by station and depth to compute PAR levels available to the *Thalassia* blades.

Carbohydrates

From the bi-monthly samplings, the rhizome fragments collected with the shoots for productivity determinations were analyzed for soluble carbohydrate determination. Approximately ten samples were processed for each station and date for a total of 457 samples analyzed.

Rhizome sections, 1-3 cm on each side of the shoot attachment point were dried, ground, and analyzed by the calorimetric trichloroacetic acid-phenol-sulfuric acid method of Dubois *et al.* (1956) using glycogen standards as described in Dawes (1981).

Biomass Cores

Four biomass collections using 12.5 cm x 12.5 cm cores were conducted during the project. A total of 320 cores was processed, ten at each station on each date. Samples were rinsed of most sediment in the fields and maintained in the laboratory at 4°C until processed.

For processing, *Thalassia* shoots were counted, and gently rinsed with deionized water to remove sediments and macrofauna. The presence of other seagrass species in the core

were noted and discarded. The below-ground detritus (fibrous remnants of blades) was removed and discarded and *Thalassia* material separated into necrotic tissue plus attached epiphytic material, productive tissue (green blades above the leaf-sheath boundary), short shoots (between leaf-sheath boundary and rhizome), and combined roots and rhizomes. Rhizome sections were measured for length and width. Any shoots connected to rhizomes were measured for the distance between oldest and newest leaf scars, and the number of scars counted. The four tissue fractions were dried to a constant weight at 103-105°C and weighed to 0.001 g.

Data were used to compute above- and below-ground biomass and ratios of *Thalassia*, tissue apportionment as percentages of total biomass (% of blades, shoots, or roots and rhizomes), and rhizome density and weight-to-length ratios. Measurements of biomass were transformed to areal units by converting core biomass data to biomass per shoot, then multiplying by the mean number of shoots observed in quadrat counts (25 cm x 25 cm, n~40) for that station and date.

Sediments

Sediment sample processing included determination of percent organics and grain size. Percent organics were determined according to Standard Methods (APHA, 1989) 2540E. The sample was homogenized by manually stirring, subsampled into a tared weighing dish, and ignited to 550° ± 50°C.

For grain size analysis, samples were wet sieved (0.063 mm mesh) with deionized water. The washed fines were retained, centrifuged, decanted, dried at 105-110°C, and the weights of this fraction recombined with the fines obtained from the mechanical sieving below. The washed coarse fraction (>0.063 mm) was oven dried at 105-110°C for a minimum of 36 hours, then mechanically sieved through a series of sieves at 2.00, 1.00, 0.50, 0.25, 0.125, and 0.063 mm to identify the distribution of material at whole-phi (ϕ) increments. Phi (ϕ) units are calculated from the sieve mesh sizes using the following formula:

$$\phi = -\log_{10}(\text{mesh size, mm}) \bullet (\log_{10}(2))^{-1}$$

Larger particle sizes are larger negative ϕ sizes, while silt/clay fractions would have ϕ greater than 4.0. Sample statistics were computed according to Folk (1974) and included mean and median gram sizes.

Statistical Testing

Statistical analysis of the data were performed using Sigmastat Statistical Analysis system Version 1.0 (Jandel Scientific, 1992) and Northwestern Analytical NWASTATPAK, Version 4.1 (1986). Two group comparisons were done by t-test and when the normality test failed, the Mann-Whitney test was selected as a nonparametric alternative.

Friedman's two way ANOVA, Kruskal-Wallis, and Wilcoxon signed rank tests were also used for analysis of much of the non-normally distributed *in situ* data. The multigroup comparisons were performed by one way ANOVA. When the normality test failed, the Kruskal-Wallis one-way ANOVA was selected as the nonparametric alternative. When the treatments were significantly different, the pairwise comparison was done by Student Newmann-Keuls as Dunn's test.

Data from Other Sources

Productivity-Irradiance Measurements

Although not a funded portion of MML project, Dr. Clinton J. Dawes, University of South Florida (USF), requested and received intact shoots from all sites, both shallow and deep stations, for the measurement of productivity-irradiance (P/E) relationships (through oxygen evolution) and tissue chlorophyll content. The measurements were conducted for both the April and June samplings, and results included with his permission in the analyses of PAR data as described below.

Intact shoots were collected and maintained in seawater and in the dark at ambient temperatures. Parameters of the P/E relationships were determined on multiple 0.5 cm blade sections taken from an un-epiphytized (younger) portion of mature blades. Sections of blades were allowed to rest prior to analysis to prevent confounding effects of wound respiration. Each station was processed in triplicate. Parameters determined included α (initial slope of the P/E relationship), P_{max} (maximum production rates, regardless of any further increases in irradiance), E_k ("saturating" irradiance, computed as P_{max}/α), and E_c leaf (compensation point of leaf tissue, where production equals respiration). Values were determined through individual curves fit by linear regression to the data at low PAR intensities from each replicate.

Chlorophyll a and b were determined spectrophotometrically by the maceration and acetone extraction method on five samples per station and date, using a larger portion of the blade (and therefore including older and potentially more pigmented portions).

Water Column Monitoring

Light monitoring data were obtained from both the City of Tampa (COT) and the Hillsborough County Environmental Protection Commission (HCEPC) for the 1994 monitoring year. Data from COT included both Secchi depths and attenuation coefficients from ten stations in Old Tampa, Hillsborough, Middle and Lower Tampa Bay. Data frequency was greater in Hillsborough Bay with 68 samplings for the year, seven of which extended into Lower Tampa Bay. Data obtained from HCEPC consisted of Secchi depths collected monthly at 54 stations through Tampa Bay. A total of 23 of the 54 HCEPC stations were located in the lower Middle and Lower Tampa Bay, with approximately ten in the general vicinity of the continuous light stations. The monitoring

data from both programs available for lower Middle and Lower Tampa Bay, however, were generally for stations farther from shore than the light monitoring stations used for this project.

Solar Irradiance

Attempts were made to find continuous records- of incident (in air) PAR data during the project year to evaluate light losses at the air-water interface. Unfortunately, sensors previously maintained by the United States Geological Survey in Tampa and the Department of Environmental Protection-Marine Research Institute in St. Petersburg were no longer in operation. The weather station at MML (= 35 km south of the study area) provided continuous incident irradiance data with a pyranometer, however, and these data were obtained to aid in interpretation of water column light levels, although the units (Watts m^{-2}) are not directly analogous to the $\mu\text{E m}^{-2} \text{ sec}^{-1}$ of the PAR sensors due to differences in spectral response between the two sensors.

Tidal Data

Selected months of continuous tidal data were available from the PORTS (Physical Oceanographic Real-Time System) network at both Port Manatee and St. Petersburg, but were not available for the entire project year or directly available for the continuous light stations at Point Pinellas, Mullet Key, or the Manatee River. Tidal variations in water depths were estimated at all locations as follows.

Tidal harmonics were derived from 697 consecutive hourly tide heights (approximately one month) using actual data recorded in the mouth of the Manatee River (CDM, 1994), Port Manatee (PORTS), and St. Petersburg (PORTS) and a tidal analysis and prediction program (Boon and Kiley, 1978; Hayward, 1993). A harmonic analysis method of least squares solves for main tidal constituents and Shureman's (1971) inference formulas are used to determine 15 secondary constituents. Constituents determined are used to generate hourly predicted heights relative to the datum of the initiating data. Data from Port Manatee and the Manatee River were used directly with no alteration in times to produce harmonics and generate hourly predicted tidal heights for PRT and RIV, respectively. Data sets used as initiating data were January 1-31, 1994, for Port Manatee and April 30-May 30, 1993, for the Manatee River. PORTS data were relative to mean lower low water, while the Manatee River data were to an arbitrary datum approximately 2.5 m below mean water level.

Continuous tidal data from St. Petersburg (available every 6 minutes) were offset by -24 minutes for all measurements to approximate the predicted tidal corrections of -22 minutes for high and -29 minutes for low tides at Point Pinellas (U.S. Department of Commerce, 1994, Figure 6). Heights were also multiplied by the given factor of 0.86 for Point Pinellas. Similarly, St. Petersburg data were offset by 2 hours and 18 minutes and heights multiplied by 0.91 to estimate tides at Mullet Key, approximately

interpolating the tidal differences of -2 hours 27 minutes / -2 hours 24 minutes for Egmont Key and -2 hours 22 minutes / -1 hours 58 minutes for the Sunshine Skyway. The respective offset and adjusted data sets were used to solve for the tidal harmonics at the PIN and MUL locations, and used to predict hourly tidal heights. Initiating data used for both locations were from January 1-31, 1993. Plots of observed and predicted data indicated close agreement (Figure 7), although as predicted data, the effects of wind or storm induced changes in water level (Figure 8) are not represented.

To compute the approximate depths of the seagrass beds sampled, water depths observed while on station ($n = 70$ per site) were subtracted from the relevant predicted tidal depths and the resultant quantities averaged to obtain the elevation of the seagrass bed relative to the tidal datum. The mean elevations of the deep edges so obtained typically had an associated standard deviation of near 0.2 m, representing a combination of sampling precision and weather impacts on predicted tides. The mean elevation obtained was then subtracted from individual hourly predicted tidal heights to convert tide levels relative to MLLW (or some arbitrary datum in the case of the RIV site) to hourly water depths over the deep edge of the sampled seagrass bed. Mean water levels over the sites were computed as the bottom elevation plus the difference between tidal datum and mean tide level. Water depths at 15 minute intervals were computed by linear interpolation between the predicted hourly values.

The difference between predicted and observed water depths (recorded on-site during each field visit) were plotted against the predicted rate of change of water depths and showed no relationship (Figure 9a), indicating that measuring depth on a rising or falling tide did not produce biases attributable to gross errors in the time offsets or height multipliers applied as described above. The effects of weather were apparent in that observed depths on days where wind velocities were greater than 5 knots were more likely to be widely separated from the predicted depths. Predicted minus observed depths displayed an inverse correlation with observed depths (Figure 9b) consistent with the underprediction of tidal extremes attributed to winds. The average **absolute** difference between predicted and observed water depths (on both windy and calm days) was 0.11 m, with maximum observed differences of approximately 0.3 m.

Predicted tidal data were used to approximate a continuous record of water column depths from which to calculate the percentages of immediately subsurface PAR received at the maximum seagrass depths. On the days when actual tides were substantially different from predicted levels due to prevailing winds, a 0.3 m decrease between observed and predicted tide height would result in an increase of 5 % (25 % versus 20 %) in the calculated percentages of PAR at depth (based on a water depth of 2.0 m and an attenuation coefficient of 0.8 m^{-1}). Typical weather patterns altering tides from predicted values, however, follow a reproducible pattern in which strong southerly winds accumulate water against the west coast of Florida, producing higher than normal tides. With northerly winds, tidal elevations are lower than predicted. Wave action typically produces decreased water clarity during each phase (subject to the fetch of individual

sites), and the errors in calculated **PAR** percentages due to underprediction and overprediction of tidal extremes should cancel over time. Analysis of MML weather data indicated only 15 days when winds in excess of 20 knots were recorded for more than one hour, indicating that the magnitude of this error, if any, is small.

PAR Data Reduction

All data recording through the project was performed with reference to Eastern Standard Time (EST). Data files were truncated by retaining only records of times between and including 0500 and 2100 hours. These times are inclusive of all times when the solar elevation is greater than 0° (above the horizon) for the entire year at this latitude and longitude (Kirk, 1994).

For any long term deployment of electronic sensors, marine fouling communities are problematic. Light sensors for a study in which water column light levels are of interest are obviously subject to errors if fouling is unchecked, and water column PAR levels could be seriously underestimated if fouling is not accounted for. The PAR data reduction included routines to measure the PAR reductions on each sensor due to fouling, and to correct individual sensor data for fouling, prior to computing water column attenuation coefficients, such that accurate values of water column clarity could be generated.

The attenuation produced by fouling communities on the PAR sensor was directly measured during each retrieval and download of the data logger. In air, a series of three sets of instantaneous readings were made both with the fouling community still in place, and with the protective clear plastic wrap removed. Top and bottom sensor readings, both before and after removal of fouling were ratioed to account for any changing ambient conditions during the measurement, and the reduction in light to the sensor effected by the fouling community computed. The fouling factor and fouling rates were computed as:

$$F_{Top} = \frac{T_{1-F}}{(T_{2-C} \bullet (B_{1-F} \bullet B_{2-F}))}$$

$$F_{Bottom} = \frac{B_{2-F}}{(B_{3-C} \bullet (T_{2-C} \bullet T_{3-C}))}$$

$$R_F = \frac{(1 - F) \bullet 100\%}{\text{days of deployment}}$$

where:

F = Fouling factor for top and bottom sensors
 T_{1-F} = Top sensor, fouled, at time = 1
 B_{1-F} = Bottom sensor, fouled, at time = 1
 T_{2-C} = Top sensor, cleaned, at time = 2
 B_{2-F} = Bottom sensor, fouled, at time = 2
 T_{3-C} = Top sensor, cleaned, at time = 3
 B_{3-C} = Bottom sensor, cleaned, at time = 3
 R_F = Fouling rate (% day⁻¹)

Approximately 45 fouling factors were directly measured for each station in this manner, with top and bottom sensors treated separately. Fouling factors averaged 0.88 (88% of true irradiance, or 12% PAR reduction), ranged between 0.37 and 1.00, and represented the proportion of PAR **remaining** after attenuation by the epiphytic community. Rates of fouling, in percentage PAR **reduction** per day, were also computed (Figure 10) and ranged between 0% and 10% day⁻¹. Heaviest fouling rates calculated were generally associated with either periods of peak barnacle and limpet larval settlement, or with fouling from egg masses deposited on the sensors. Fortunately these extreme instances were relatively rare and fouling rates averaged approximately 2 % of PAR reduction per day overall.

For station visits when the frame and sensors were not retrieved to the boat, plastic wrap was changed, but no direct measurement of fouling attenuation on individual sensors could be determined. A rate of fouling for the trips with no direct measurement was computed by linear interpolation between the previous and following measured fouling rates. Fouling factors were then computed using the interpolated or measured fouling rates and the number of decimal days the sensor had been deployed since the last cleaning. Computed fouling factors were individually examined for reasonableness and compared to logbook observations of density of fouling and relative fouling on top and bottom sensors.

Fouling factors for each 15 minute data interval were computed through linear interpolation, with the endpoints of no fouling (factor = 1.00) at the time of cleaning and the fouling factor (computed or measured) of less than 1.00 at the time of the next cleaning. While fouling growth and subsequent attenuation is more likely to proceed exponentially, linear interpolation was desirable since most fouling factors were close to 1.00 (*i.e.*, very slight correction needed), and since a linear correction was more conservative, *i.e.*, a linear correction would underestimate rather than overestimate the amount of light received.

Applied fouling corrections will only alter calculated attenuation coefficients if the fouling rate of the upper sensor are different from that experienced by the lower. Evaluation of the measured fouling factors ($n = 180$) indicated that for nearly 80% of the observations, the upper and lower sensors' fouling factors agreed within $\pm 10\%$. As

a result, a high degree of confidence may be placed in the seasonal means of fouling-corrected attenuation coefficients, and subsequent calculations from the coefficients.

All sensor data were subsequently corrected by dividing the observed sensor readings by the interpolated fouling factors (specific for both top and bottom sensors). Water column attenuation coefficients were calculated from corrected sensor data and were additionally examined for reasonableness both immediately before and after cleaning to see that abrupt changes in water column clarity were not artificially produced by interpolated fouling rates. Absolute levels of light received at the deep edge were computed by integration and summation of the individual 15 minute averages of the bottom sensor over the various time periods of interest.

Corrected top (E_T) and bottom (E_B) sensor irradiance data (sensors separated by 0.5 m) were used to compute corrected scalar attenuation coefficients (K_0 , 15 minute averages) as follows:

$$K_0 = \frac{-\ln(E_B \cdot E_T^{-1})}{0.5}$$

Each computed attenuation coefficient and station mean water level at the deep edges was used to solve for **the PAR remaining at the bottom of the water column (% PAR_w as a percentage of the immediately subsurface scalar irradiance ($E_0(\phi)$),** by substituting z (mean station depth) for 0.5 m.

$$\% \text{ PAR}_w = e^{-K_0 z} \cdot 100\%$$

The percentage of PAR so calculated represents water column processes only, and does not include reductions of incident solar irradiance due to air-water surface reflection. As wind and wave conditions and solar elevation will alter the percentage of reflection, and as these properties are not subject to management actions, the percentage reduction by the water column alone was the appropriate goal of the study. Annual or seasonal light percentages were computed as the mean of percentages received, rather than from annual mean attenuation coefficients. Implicit in the calculation of light levels at other depths is the assumption that the water column is well-mixed and homogenous from surface to bottom.

Site- and time-specific interpolated water depths obtained from tidal data were also used to compute percentages of light remaining at the bottom of the water column under tidal conditions. The percentages were again averaged over seasonal and annual periods.

Percentages and absolute levels of light at shallow stations were estimated from the assumptions that attenuation coefficients were equivalent at deep and shallow stations within a given site, and that water levels at shallow stations were 0.9 m less. Changes

in light climate due to reduced bottom reflectance at vegetated stations could not be included in the estimates for shallow sites.

$$\% \text{ PAR} = e^{-k \cdot (z - 0.9)} \cdot 100\%$$

The effects of epiphytic attenuation were also incorporated in calculations of both absolute PAR amounts and remaining PAR percentages. The epiphytic attenuation determined on ten shoots from each station and depth were used to compute a mean epiphytic attenuation specific for station, depth, and date. The epiphytic attenuation was assumed to apply to a time period beginning midway between the date in question and the prior determination of epiphytic attenuation and extending to a point midway between this date and the following determination of epiphytic attenuation. Bottom sensor data and percentages of PAR available, already corrected for sensor fouling, were further reduced by the amount of PAR reduction effected by epiphytes to simulate the % PAR, actually available to *Thalassia* blades.

$$\% \text{ PAR}_t = \% \text{ PAR}, \bullet (1 - \text{Epiphyte Attenuation} \bullet 100^{-1})$$

The bottom sensor data, reduced by epiphytic cover, was again integrated and summed to determine absolute PAR levels received by *Thalassia*.

Total attenuation coefficients, K_t , were computed using the mean station water depths (z), as:

$$K_t = \frac{-\ln (\% \text{ PAR}_t)}{z}$$

Total attenuation coefficients, representing water column PAR attenuation over finite depth plus attenuation through a comparatively very thin epiphytic layer, cannot be used to extrapolate light climates to other portions of the water column. The values, however, are useful for interstation comparisons and to evaluate the effectiveness of accounting for epiphytic attenuation, plotting K_t against maximum depth limits and typical Beer-Lambert depiction of isolumes.

Calculations of absolute light levels received by seagrasses made use of all available data points from 0500 hours until 2100 hours. It was noted, however, that attenuation coefficients, K_0 , often became quite erratic during early morning and late afternoon, in patterns beyond the expected diurnal variations associated with changing solar elevation as reported by McPherson and Miller (1994), Moore and Goodman (1993), Miller and McPherson (1993). While diurnal variations in K_0 , are expected as angle of solar incidence increases and the path of collimated light in the upper water column is actually larger than is represented by the vertical separation of the sensors, the noise in calculated K_0 was attributed to low light levels magnifying the effects of any sensor variations. To avoid biasing station averages computed, and to maintain the highest correspondence with

other Bay monitoring programs, seasonal and annual averages of K_0 presented are based on data only between 1000 and 1400 hours. Attenuation coefficients for all available times were used, however, in calculating total PAR received and time above critical values.

Bottom Reflectance

Bottom reflectance was of concern in this project due to the use of 4π sensors deployed near the bottom of the water column for the determination of attenuation coefficients. (Scalar sensors were selected for the project, as this measurement was more representative of the light available for photosynthesis.) In the event of substantial bottom reflectance, a series of PAR readings determined near bottom will appear to experience less attenuation (lower attenuation coefficient) over a specified distance than readings similarly determined in the upper portions of the water column or over the entire water column, even if the water column is homogeneous. The effect will be visible in both 2π and 4π sensor data but is most evident in spherical collector data. Using the artificially low attenuation coefficient to compute the percentage of subsurface PAR present at depth will generate an artificially higher percentage than if an attenuation coefficient for the entire water column had been used. The potential error is magnified when the attenuation coefficients are applied to increasing water column depths and is lowest when sensors are deployed across a large proportion of the water column.

Bottom reflectance is obviously a function of bottom type, with more reflectance possible from light colored sandy bottoms than from darker substrates. Substrate “darkening” by the presence of vegetation will also reduce reflectance. Reflectance is also largely a factor of the character of the light field which reaches the bottom. Reflectance is minimized when the diffuse component of the light field is high, as when particulate load or turbidity is high, when attenuation coefficients are high, when sun angle is low, when wave action is present, or under cloudy or hazy skies. As a result, reflectance is most likely under conditions of sandy bottom, calm surface, midday, and high water clarity.

Bottom reflectance, however, must be distinguished from upwardly scattered light (upwelling light) which is produced by the interaction of downwelling light and water molecules or, to a lesser extent, particulates. Upwelling light is present at all depths in the water column and is not an exclusive function of bottom reflectance. Upwelling light is attenuated similarly to downwelling light, and typically consists of between 4-10% of downwelling light (Kirk, 1994). Irradiance reflectance (upwelling:downwelling light) also increases with any phenomena which increases the scattering proportion of attenuation; generally with increasing turbidity, increasing attenuation coefficients, with depth, and has been observed as high as 24% (Kirk, 1994). Scattering:absorption ratios for Tampa Bay would lead us to expect irradiance reflectance values on the order of 7-15%.

Bottom reflectance in this study was evaluated by comparison of 2π and 4π attenuation coefficients, manually determined over the entire water column on approximately 20 occasions per station. Sampling dates included both clear and turbid conditions. Theoretical observations are that ratios of K_d (diffuse attenuation coefficient [2π sensor]) to K_0 (scalar attenuation coefficient [4π sensor]) should range between 1.01 and 1.06 under the range of scattering expected for Tampa Bay waters (Kirk, 1994).

Cosine attenuation coefficients were slightly higher than expected from theoretical considerations, averaging 1.13 of the manually determined scalar attenuation coefficients, or 0.08 m^{-1} higher. No differences were observed between the relationships for individual stations. Linear regression of all data produced a highly significant relationship ($p < 0.001$) with an empirical equation of:

$$K_d = 0.097 + 0.966 \bullet K_0$$

Although a consistent (and expected) bias was observed between the data types, 88% of all data pairs were within the $\pm 1 \sigma$ (0.16 m^{-1}) determined for replicate field profiles in Sarasota Bay (Dixon and Kirkpatrick, 1994). As a result, while the difference between cosine and scalar attenuation coefficients is significantly ($p < 0.001$) different from zero, the numerical bias is substantially less than expected measurement precision.

More precise estimates of bottom reflectance could be obtained from irradiance reflectance (downward-facing 2π sensor: upward-facing 2π sensor percentages) computed at all measurements depths. Reflectance at surface depths should be minimally impacted by bottom reflectance, while measurements made near the bottom were expected to show increased upwelling:downwelling ratios if bottom reflectance were a significant phenomenon.

Irradiance reflectance at surface depths (0.2 m) averaged 5.6% well within ranges reported by other investigations (summarized in Kirk, 1994). Station averages of reflectance near the surface were comparable, ranging between 4.8 and 6.7 %. Irradiance reflectance at the depths closest to the bottom of the deep stations, on the other hand, averaged 15.8%. The difference between 5.6% and 15.8%, or 10.2%, is taken as an approximation of the bottom reflectance, or the amount of PAR reaching the bottom which is redirected upwards into the water column. No station had any single bottom reflectance estimate in excess of 15.9 %. Bottom reflectance values at the vegetated (darker substrate) shallow sites averaged less than 2%.

An approximate model of scalar attenuation in the presence of bottom reflectance was constructed in which K_d was selected based on station means and used to attenuate downwelling (2π) light, irradiance reflectance (backscatter) was assumed constant at 5 % of downwelling light, bottom reflectance was assumed to be a fixed percentage of the downwelling light reaching the bottom (which was subsequently attenuated in an upward direction using the same coefficient used for downwelling light. The sum of

downwelling, upwelling (backscattered), and bottom reflected light was used to approximate a scalar profile of irradiance, such that the effects of bottom reflectance could be assessed. Using a 2.0 m total water column depth, 10 % bottom reflectance, and a K_d value of 0.82 m^{-1} , a K_0 computed from sensors within 0.2 m of the bottom and separated by 0.5 m is 0.03 m^{-1} lower than a K_0 computed over the entire water column depth. Resulting calculations of percentages of PAR at depth differed by only 1.1% (22.5 % for measurements near bottom, 21.3 % using entire water column measurements). Bottom reflectance of up to 15.9 % (the maximum observed) produced differences of less than 2% in the PAR calculated at depth.

In addition, the difference between the two percentage values is likely to be overly large as the angular component of both upward and downward propagating light is neglected in the estimation. If the angular components were included, they would result in a larger increase in the downwelling component than in the backscattered or reflected, and would thus further reduce the differences between the two attenuation coefficients and calculated PAR percentages. In light of the magnitude of the maximum potential error, and the fact that measurements to evaluate bottom reflectance were made near midday when reflectance was expected to be the greatest, no further corrections for this effect were employed.

RESULTS

Data Completeness

Deployment of continuous light sensors extended over an elapsed period of between 369 and 372 days for each of the sites. Approximately 157,000 observations of PAR were performed during daylight hours, or an average of 4900 hours of data per sensor per site on average. Data completeness was calculated as 90% overall. The MUL site was 85 % complete for both top and bottom sensors; PIN was 100% for the top sensor, and 96% for the lower; PRT was 86% and 84% complete for top and bottom, respectively; the RIV site was 93 % complete for the upper and 96% complete for the lower sensor. Missing data blocks unfortunately included some of the periods during which growth measurements were determined for both February and April for the RIV site, and in December at PRT, and are listed in Table 2 at end of text.

Light Climate

Representativeness of Monitoring Year

Net Change in Areal Extent

The light climate measured during the project year and conclusions drawn from the measurements, will be more robust and useful if 1) the areal extent of the measured grassbeds was stable and if 2) the water column clarity during the year was comparable to conditions during the years immediately prior. Light climate data generated during a period when *Thalassia* “retreats” will be presumed to represent an end-member, *i.e.*, the amount of light received was not enough to maintain *Thalassia* at depth, even in the absence of catastrophic factors such as storms, salinity extremes or disease. In addition, the collected data will be most useful if the water clarity is as close to “typical” as possible. While unusually low attenuation values for a year may permit immediate expansion or increase in density, it has been demonstrated (Hall *et al.*, 1991) that *Thalassia* located at the deep edge of bed could, when shaded, overcome light stresses as much as 13 months later by presumably drawing on rhizome reserves.

The areal extent of the grass beds was not directly measured to a universal horizontal coordinate system, as the “edge” of a *Thalassia* bed is frequently an ambiguous demarcation. Density of shoots and total biomass per unit area gradually decreases with proximity to the edge, whether in response to sediment depth (Zieman, 1982), water depth and therefore light (Buesa, 1974, 1975; Kemp *et al.*, 1988; Hall *et al.*, 1991), or other limiting factors. Even at the point where the bed may be said to have “ended”, a single rhizome and regularly spaced associated shoots can be seen to extend into an otherwise unvegetated area. During this project, for example, additional quadrat counts determined shoot densities to be either 10 m^{-2} or 30 m^{-2} , depending on which side of the

edge boundary the quadrat was placed, although the 0.0625 m² quadrat was touching the “edge” in both instances. Approximately 1 m from the edge toward the center of the bed, shoot densities were on the order of 65-70 m⁻².

The project used fast marks and determined shoot density and other biomass-related parameters at reproducible locations to determine whether increases or decreases had occurred. The task is made more difficult by a strong seasonal signal in both parameters, and by intra-annual variations in temperature or salinity which may also affect biomass.

Quadrat counts of shoot density and above-ground biomass from individual shoot weights and quadrat counts were performed at deep stations during each of the six field efforts for growth determinations. Shoot densities ranged between 36 and 109 m⁻² and biomass between 3.3 and 32.5 g m⁻². Many of the 0.0625 m² quadrats contained no shoots. Transformed data were often non-normal and so non-parametric tests (Kruskal-Wallis and Friedman’s two way ANOVA) were used to test for similarity between the initial (December 1993) and final (October-November 1994) densities and above-ground biomass.

The sites designated MUL-D and RIV-D displayed no significant net changes in shoot density over the study. Density at PRT-D nearly doubled ($p < 0.001$), while counts at PIN-D were significantly reduced ($p < 0.001$) by nearly one-third. Typical patterns of shoot density and biomass (Iverson and Bittaker, 1986; Phillips, 1960; Durako and Moffler, 1985; Tomasko and Dawes, 1990; Hall *et al.*, 1991) would lead one to expect a winter decrease in both biomass and shoot density as temperatures drop and day length shortens. When the expected pattern is applied to the data available for this study, changes expected for a stable grassbed would include a net increase in both biomass and density between initial and final samplings as temperatures during the final October-November sampling were still well above the thermal minimum observed during January sampling.

The level of significant change in shoot density between initial and final samplings at PIN and PRT were in both instances much less than the annual variation. The net difference in mean shoot density at the two sites equated to an average change of -1.2 and + 1.8 shoots quadrat⁻¹ for PIN and PRT, respectively. In addition, biomass levels between initial and final samplings displayed conflicting patterns at some sites. Biomass at the deep edge of MUL was unchanged between initial and final samplings, was significantly higher at PIN and PRT ($p < 0.001$), and was lower at RIV ($p < 0.05$). Decreases in biomass at RIV may be linked to heavy rains and freshwater discharge from the Manatee River which occurred in late August and September as the shoots at this station had obviously been defoliated not long before the final sampling. Increases in biomass at PIN and PRT are consistent with expected seasonal patterns, but at PIN, biomass increases appear to be linked to a shade adaptation brought on by lowered ambient PAR (see discussions below).

Results of reconstructive aging analyses, because of the minimal numbers of shoots processed, should be viewed with caution. The number of shoots for MUL, PIN, RPT, and RIV were 88, 44, 71, and 91, respectively. The low numbers of shoots in any leaf scar class interval made selecting the modal value of annual cohorts somewhat subjective, although the agreement between the mean annual numbers of blades produced (determined by average cohort interval) and the independently determined plastochrone interval in the present study, agreed very well. For all deep stations, no significant station-to-station differences in shoot distribution by year classes were observed (Kolmogorov-Smirnov, $p > 0.05$).

The MUL site was noteworthy in that no shoots of the 0-1 year old class were sampled and, as a result, gross recruitment was calculated as zero and net shoot production was a negative value. The calculations are very sensitive the absence of this datum, however, as the presence of a single shoot of less than 1 year old would have brought the gross recruitment and net production figures into line with all other stations. Typical mortality values were 0.17-0.22 In units year⁻¹ at the four deep stations. Annual net shoot production calculated as -0.1 to -0.2 shoots year⁻¹ for all stations except MUL, which, with no shoots younger than a year, had an estimated net annual shoot production of -1.2 shoots year⁻¹, the calculated mortality rate. The oldest shoots observed at the sites appeared to be 14.9, 11.5, 10.6, and 11.2 years for MUL, PIN, PRT, and RIV, respectively, while the mean ages of the shoots collected at the sites were 5.9, 3.6, 4.0, and 3.7 years. The beds at PIN and RIV are apparently comparatively young.

The average inter-cohort distance as well as plastochrone interval was unusual for PIN, in that cohort data produced average values of 8.1, 6.5, 9.6, and 9.7 blades year⁻¹, for MUL, PIN, PRT, and RIV, respectively, while measured plastochrone interval was 8.1, 6.6, 9.2, and 9.9 blades year⁻¹ for MUL, PIN, PRT, and RIV, respectively. Lower blade production rates at PIN-D are coupled with a dramatic increase in mean blade length for this station in August and October. These characteristics may represent an early response to reduced light levels at PIN-D (in comparison to other stations) and are further supported by the lower below-ground biomass observed at this station.

In conclusion, changes at the deep edges of three of the sampling sites were, in general, consistent with the normal seasonal patterns of biomass. Increases in biomass between initial and final samplings are attributed to the comparatively warm fall and early winter during the last portion of fieldwork for this project. As temperatures drop, ex-foliation might be expected to result in lowered biomass values. At PIN, decreased shoot density values from the beginning to end of the project, increased blade length, reduced below ground biomass, and reduced blade production rates are more indicative of a response to lowered PAR and a slight “retreat” of the deep edge at this site. The level of change while significant, however, is very slight and the long term effects of the lower PAR received at this station are unknown.

Salinity

Results from surface salinity samples collected during each maintenance visit appear in Figure 11. Annual averages for MUL, PIN, PRT, and RIV were 30.6 ppt, 28.7 ppt, 29.4 ppt, and 28.9 ppt, respectively. Again the annual values were well within the ranges depicted for 1980-1990 in King Engineering Assoc. (1992), and not surprisingly, MUL, as closest to the mouth of Tampa Bay recorded a slightly higher salinity. Seasonal patterns between the project and long term averages are similar as well, with a slight depression in salinity evidenced in February in both project data and historical monthly averages, prior to the onset of the larger wet season in summer and fall.

Salinity minima were observed during October, comparable to long term seasonal patters (King Engineering Assoc., 1992). All four stations exhibited comparatively low salinities that were associated with several large weather systems and rainfall totals that were received in August and September. During this period, salinities at all sites were below the 24 ppt optimum described by Phillips (1960), McMillan and Mosely (1967) and Zieman (1975) and were 2-5 ppt lower than the September averages depicted in King Engineering Assoc. (1992). Bottom salinities were not observed to fall below 17 ppt, however.

The RIV site in particular was heavily influenced by discharge from the Manatee River, as can be seen by the abrupt decreases in salinity of 5 ppt or more. Under an extreme discharge event, the river stratified with respect to salinity, and surface to bottom differences in salinity of up to 17 ppt (surface salinity 10 ppt, bottom salinity 27 ppt) were recorded during the project. Freshwater during the August-September period at the RIV site was apparently responsible for an abrupt defoliation and decrease in biomass, based on the appearance of the remaining blades. Surface salinity at the PRT site also abruptly decreased on one occasion. Freshwater influencing the PRT site may originate as coastal drainage or from the mouth of the Little Manatee River to the north.

Temperature

Temperatures recorded during the project (Figure 12) were very comparable between stations with MUL, PIN, PRT, and RIV reporting project averages of 23.7°C, 24.2°C, 25.0° C, and 24.2 °C, respectively. The values are well within the envelope described by the 1980-1990 data summarized by King Engineering Assoc. (1992) for middle Tampa Bay. Comparisons with described monthly patterns also indicate that the project year was slightly (1-2°C) colder during January 1994, than a 17 year record illustrates, and observed temperatures were in the lowest range of temperatures recorded at St. Petersburg (McNulty *et al.*, 1972). The lowest temperatures recorded (10.8°-12.7°C) were below the 15°C reported as producing leaf kill (Zimmerman and Livingston, 1976). Temperature during the late fall and early winter (November-December 1994), however, were as much as 4-5 °C warmer than historical averages.

Temperatures during July and August were greater than the 29°C of the long-term averages (Ring Engineering Assoc., 1992), and maximum values were similar between stations, ranging from 31.5° C at PIN to 33.0°C at PRT. Zimmerman and Livingston (1976) report defoliation at 30°C, although Barber and Behrens (1985) indicate growth is not inhibited up to 31° C. Abrupt temperature decreases (= 5° C per week) were noted with the passage of frontal systems or extended periods of cloud cover, while typical diurnal variations were on the order of about 1°C.

Water Clarity

To assess whether water clarity during the monitoring year was typical, the Hillsborough County Environmental Protection Commission (HCEPC) provided secchi depths for the 1994 monitoring year. Secchi depths in inches were averaged by station for the year (Table 3) and compared to the long-term averages as presented in King Engineering Assoc. (1992), Figure 13. Secchi depths at individual stations in Lower Tampa Bay during 1994 were very comparable to 1989-1990 values. Middle Tampa Bay data during 1994, as well, were similar to a period from roughly 1986-1990. Secchi depths during 1994 in Hillsborough Bay, however, demonstrated a continuing improvement which appears to have continued almost without interruption since 1979. Individual station means in this segment were between 5 and 10 inches deeper than the last reported annual mean Secchi depths for 1990. More recent general trend depiction in water quality by Bay segment (HCEPC, unpublished data) supports these conclusions.

Water clarity in Middle Tampa Bay and Lower Tampa Bay appears consistent with historical data. Attenuation coefficients measured at the continuous light sites are representative of long-term conditions. Under a stable water clarity regime, light-limited grass beds are also expected to be stable, and the light levels measured at depth will represent the minimum light requirements for *Thalassia*. Water clarity conditions in Hillsborough Bay, however, are apparently still improving, a conclusion consistent with the increasing coverage of Halodule (Avery, 1991) noted for this segment. With the lag times for recolonization, seed stocks, and limitations to vegetative transfer of *Thalassia* unknown, it is possible that water clarity may be sufficient to support *Thalassia* or other SAV, and yet the species may still be absent.

Attenuation Coefficient Characteristics

Diurnal and Seasonal Patterns

The highly variable nature of the underwater light field was clearly visible in the PAR data received by both upper and lower sensors and in calculated attenuation coefficients. Examples in Figures 14-17 are for the periods during which above-ground seagrass growth was determined. The bulk of the variation is attributed to changing incident irradiance, of both annual and diurnal patterns of solar elevation and fluctuations in cloud cover (Figure 18), as illustrated by the MML weather station. Storm effects and

recovery are also quite apparent both in absolute PAR levels and in attenuation coefficients (See March 3, 1994, Figures 14-17). While less daily variation was apparent in the calculated attenuation coefficients, distinct diurnal patterns described by Moore and Goodman (1993) and McPherson and Miller (1994) were also evident. The increase in K_0 observed in early morning and late afternoon, and the minimum K_0 observed at midday, is attributed not only to an increased light path (between sensors at a fixed vertical distance) at low solar elevations, but also the increasingly diffuse irradiance when the sun is not directly overhead. The diurnal midday minima in K_0 were repeated throughout the year and were most noticeable during summer when the diurnal range in solar elevation is at a maximum (Figure 19).

As the emphasis of this study was to determine the light received at the deep edge of selected seagrass beds, K_0 was not corrected for sun angle. The correction is appropriate when endeavoring to link the absolute attenuating properties of the water column to analytical parameters (color, chlorophyll, turbidity, etc.), but is unnecessary when K_0 is to be used to compute percentages of light at varying depths. Comparisons of K_0 determined at the continuous sites with other monitoring programs was conducted only with measurements from between 1000 and 1400 hours, when diurnal variations are small, and correction for sun angle typically considered unnecessary.

Monthly means of attenuation coefficients determined between 1000-1400 hours appear in Figure 20. Some months have large associated deviations attributed to storms (March, MUL and PRT), drift algae obscuring the sensors (May and June, PIN; June, RIV), or the discharge of highly colored water and subsequent tidal mixing (October, RIV). The signature of drift algae on the data is one of abruptly varying K_0 values at periods much shorter than would be expected for tidal variations in water masses. Fortunately, the periods when drift algae were noticeable were quite few. The K_0 values, while not accurately representing water column attenuation, were left in the data base to include whatever impacts that drift algal shading produced. Changes in K_0 as the result of different water masses and resultant changing water clarity are more gradual and often cyclical.

The seasonal pattern in K_0 values is similar to that measured in Sarasota Bay to the south (Dixon and Kirkpatrick, 1995), in that maximum water clarity occurred in winter and early spring (December through April or May). By May or June, water clarity declined (k increased), and was attributed to seasonal increases in chlorophyll and color values typically observed during the wet season (King Engineering Assoc., 1992). The seasonal signature was less evident at the PIN site, which was marked by high attenuation during May and June with K_0 values during the remainder of the year only slightly higher than during the winter. Seasonal patterns were slightly different and more varied in long term data (King Engineering Assoc., 1992), in which some Lower Tampa Bay stations were marked with increases in water clarity (decrease in K_0 during the summer months).

Annual Means

Annual means were computed both as overall means (from December 1, 1993, to November 30, 1994) and as the mean of monthly means ($n = 12$) to lessen the weighting potentially produced by missing data. Annual mean attenuation coefficients (between 1000-1400 hours, and as the mean of monthly means) were 0.84 m^{-1} , 0.80 m^{-1} , 0.84 m^{-1} , and 0.94 m^{-1} for MUL, PIN, PRT and RIV, respectively (Table 4). Computed as the mean of all data (between 1000-1400 hours), annual K_0 values were 0.83 m^{-1} , 0.80 m^{-1} , 0.86 m^{-1} , and 0.98 m^{-1} for the four stations, varying only slightly from the mean of monthly mean computations. Median values of all data pooled were 0.76 m^{-1} , 0.73 m^{-1} , 0.78 m^{-1} , and 0.88 m^{-1} for MUL, PIN, PRT and RIV, respectively. Standard deviations were large, comprising between 50% and 70% of the means, and represent the seasonal fluctuations in water column clarity. Based on the biological parameters, a growing season of May through September was also defined, and mean attenuation coefficients recalculated as above. Values for the four stations were somewhat larger during the growing season, at 0.97 m^{-1} , 0.96 m^{-1} , 0.89 m^{-1} , and 1.17 m^{-1} , with standard deviations again large, between 40% and 80% of the mean values.

Comparison between Stations

Inter-station differences were evaluated by examining the differences of individual station attenuation coefficients from the mean of all stations at each 15 minute interval. Only times where all four station data points were available and during the hours of 1000-1400 were used. Distributions were non-normal and non-parametric tests (Kruskal-Wallis) used to examine differences between stations both for the project year and quarterly periods (December-February, March-May, etc.). With only two exceptions, all sites were significantly different from one another during all quarterly periods and for the project as a whole ($p < 0.001$). During the summer quarter (June-August), PIN was significantly different from PRT at the 0.01 level, while during the winter quarter, PRT and RIV were not significantly different. In this data set, attenuation coefficients at RIV averaged 0.15 m^{-1} higher than the mean of all stations, while the remaining stations were between 0.02 and 0.07 m^{-1} lower than the four-station mean.

Station Water Depths

Station water depths, determined from predicted tides, observed water depths while on station, and computed station elevations appear in Table 5. The standard deviation of depth estimates is approximately 0.15 - 0.20 m (standard error of 0.02 m), or approximately the same order of magnitude as the accuracy of tidal predictions. Figure 21 illustrates the relationship between maximum depth limits and annual attenuation coefficients for the four stations in Tampa Bay. Superimposed in Figure 21 are comparable data from Sarasota Bay (Dixon and Kirkpatrick, 1995). The Sarasota Bay data are composed of an annual record of biweekly determinations of attenuation coefficients ($n = 26$) at the deep edges of both *Thalassia* and *Halodule* beds and serve

to illustrate that there are additional influences besides average water column clarity that control the maximum depths to which seagrasses extend.

An important point is the datum to which water levels refer. The initial column in Table 5 refer to depths of the water column over the deep edge of the continuous light sites, equivalent to elevations from a vertical datum set at the elevation of the deep edge of each *Thalassia* bed. The mean water column depth is biologically relevant in that it is the average distance over which PAR is attenuated. Bathymetry data, navigational charts, PORTS tide data, 1950 and 1990 seagrass mapping, and Tampa Bay National Estuary Program (TBNEP) resource mapping and seagrass depth targets (Janicki *et al.*, 1994), however, are all referenced to a mean lower low water datum (Gulf Coast Low Water Datum).

For the stations around Tampa Bay for which tidal differences are available, mean tide level is between 0.30 m and 0.37 m higher than MLLW (U.S. Department of Commerce, 1994). To adjust the continuous light sites to an approximate MLLW vertical datum, therefore, water column depths were all reduced by 0.34 m. The resulting elevations have little biological meaning, are not used for the calculation of percentage of ambient PAR remaining at depth in this report, and are presented only for comparison of stations with seagrass restoration targets.

Percentages of PAR

Water column depths, together with attenuation coefficients, were used to compute the percentage of subsurface scalar PAR reaching the maximum depth limits for each 15 minute reading (Table 6). Percentages were computed using both the fixed station depths given in Table 5, and the predicted tidal heights to evaluate the potential magnitude of differences in light climate produced by changing tidal amplitude. Percentages were averaged over months and year as for the attenuation coefficients above, again only using values from data gathered between 1000-1400 hours.

The effect of tidal phase varies by month, with average percentages slightly higher for some and slightly lower for others, dependent on whether daylight low or high tides predominate. The absolute value of the differences average less than 2 % , with the tidally varying percentages for this year averaging **0.5** % larger than the fixed depth percentages, overall. Annual mean PAR percentages (as the mean of the monthly means) ranged between 20.5% and 23.5% for the individual sites for fixed depth computations and between 21.0% and 24.2% for the tidally varied data. The mean between stations was **22.5%** of fixed depth data and 22.7% for tidally varied data. The value of 22.5% for annual light requirements and fixed depth computations was used for the remainder of the data analysis as being more conservative (from the standpoint of nutrient load reductions).

The reduced water column clarity during the growing season was reflected in percentages of PAR received at the deep edge during May to September, and are also shown in Table 6. Fixed depth, and mean of monthly mean computations were again used and deep edge stations received an average of between 14.5 % and 18.0% of subsurface scalar PAR during the season of peak growth. The interstation mean was 16.1% , which was used to evaluate the other regions of Tampa Bay.

Water Column Characterization of Shallow and Deep Stations

Water column profiles of PAR were performed during each field visit and used to assess the water column comparability between the shallow and deep stations of each site. Values agreed on average within 0.07 m^{-1} , with only nine instances out of 240 where the difference between $K_{0\text{-deep}}$ and $K_{0\text{-shallow}}$ was 0.50 m^{-1} or greater. There was no overall seasonal pattern to differences, except that largest disparities in water column clarity between shallow and deep stations were in the summer and fall, with the shallow stations more turbid.

Paired t-tests were performed to detect similarities between stations. Differences between deep and shallow site water column clarity were not significant at either MUL or PRT. At RIV, initially significant differences ($p < 0.05$) were no longer apparent once two statistical outliers (Sokal and Rohlf, 1981) were removed. It appears that, in the absence of extreme flows, shallow and deep sites at RIV were also very comparable in water column clarity. At PIN, however, differences were significant at the 0.01 level, attenuation coefficients at the shallow station averaging 0.12 m^{-1} higher than at the deep location of this site. Significant differences remained even after the removal of two outliers (Sokal and Rohlf, 1981), when the shallow station still averaged 0.09 m^{-1} higher coefficients.

The conclusion is that significant differences in water clarity exist between shallow and deep stations at PIN. With an attenuation coefficient from the deep station of 0.8 m^{-1} , and depth of 1.4 m at the shallow site, PAR light levels at the shallow site could be overestimated by approximately 5% of subsurface scalar PAR. The variation in K_0 across very short horizontal distances serves to illustrate the importance of site specific data, and to caution against transferring water clarity measurements from mid-Bay stations to nearshore environments. Despite the consistent bias, no adjustment to K_0 was made before calculating light levels at the shallow site, as light at the shallow station was not considered limiting.

Epiphytic Attenuation

Epiphytic cover has been found to reduce PAR available for photosynthesis (Day *et al.*, 1989, Kemp *et al.*, 1988, Sand-Jensen and Sondergaard, 1981) through attenuation and by so doing, to result in reduced productivity (Tomasko, 1993a). Epiphytic communities have been demonstrated to have a broad absorption spectrum with no marked regions of

transmittance or absorption except for a generally increased absorption at higher wavelengths (Neckles, 1993). As a result, overall PAR attenuation of an epiphytic suspension is an appropriate approximation to calculate the PAR which is available to the *Thalassia* blades, in the absence of more rigorous spectral attenuation information for water column and epiphytes, as well as the photosynthetic action spectra of *Thalassia*.

The reduction in PAR is an exponential relationship with epiphytic loads for numerous species (Bulthuis and Woelkerling, 1983; Sand-Jensen and Borum, 1983; Neckles, 1993; Kemp *et al.*, 1988) and is again demonstrated for *Thalassia* in Tampa Bay (Figure 22). (As only the light attenuating properties of the epiphytic community was investigated during the project, no separation or distinction was made between epiphytes and epifauna, and the term epiphytes and epiphytic materials refers to all materials and organisms which were scraped from the *Thalassia* blades.) Relationships of ash free (AF) epiphytic biomass with PAR attenuation are somewhat better than for dry weights, and the empirical relationship (Figure 23) takes the form of:

$$\% \text{ Epiphytic Attenuation} = 52.91 + 19.11 \bullet \ln (\text{AF Epiphytes } \text{cm}^{-2})$$

Implied is that the organic fractions contribute more directly to attenuation than do the inorganic fraction of epiphytes, despite the fact that ash free weights are only approximately 20% to 40% of the total epiphytic load.

The epiphytic load on *Thalassia* blades generally exhibits a consistent seasonal pattern of increased epiphytic biomass during winter periods of low growth (Leverone, 1991; Lapointe, 1992; Dixon and Kirkpatrick, 1995). When blades are growing more rapidly, colonization rates of epiphytic species are apparently insufficient to keep pace, and proportions of epiphytic biomass decreases (Zieman and Zieman, 1989). Other factors such as nutrient supply, grazing removal rates, PAR, temperature, and currents may also play a role in regulating epiphytic growth (Neckles, 1993). The relatively consistent rates of fouling on an artificial surface during the year (PAR sensors, Figure 10 above), however, would indicate that seasonal patterns of blade growth and etiolation are a major factor in controlling annual patterns of epiphytic density at a given location.

Seasonal patterns of epiphytic attenuation during this study (Figure 24, Table 7) were slightly unusual in that epiphytic growths, while initially heavy in December and January, and decreasing as expected during the spring and summer growing season, remained low throughout the fall (October sampling). This is attributed to the fact that above-ground growth was still continuing (see discussion of above-ground growth, below), that the average age of leaves on shoots was younger than during the winter and early spring, and that water temperatures were some 4-5°C above normal in the fall. Annual average epiphytic attenuation ranged between 32.0% and 36.2% at the deep edge.

Annual averages of epiphytic attenuation for the Lower Tampa Bay stations (32-36%) were substantially less than for Sarasota Bay (Dixon and Kirkpatrick, 1995), where

epiphytic attenuation averaged near 50%. During the growing season, attenuation due to epiphytes at the Tampa Bay stations was even lower, near 20%. As increasing epiphytes have been determined to reliably reflect increased nutrient loads (Tomasko and Lapointe, 1991; Dunton, 1990; Neckles *et al.*, 1994; Neverauskas, 1987; Silberstein *et al.*, 1986; Lapointe *et al.*, 1994), at times even more so than water column chlorophyll levels (Borum, 1985), the total nutrient loads relative to receiving water volumes and flushing time may be greater for the lagoonal Sarasota Bay system.

Comparison of deep and shallow stations determined that when significant differences existed at a site, the shallow stations were more likely to have a heavier epiphytic covering (Figure 25). This pattern is in contrast to other authors (Leverone, 1991; Kemp *et al.*, 1988), who have determined a positive correlation of epiphytic load with depth, but is in concert with the findings of Tomasko and Lapointe (1991), in which under nutrient enriched conditions, epiphytic loads were greater under higher ambient light conditions. For Tampa Bay, the largest differences between shallow and deep stations were noted at PIN and at RIV (Figure 26). The shallow station was heaviest in epiphytic load at PIN during the wet season and could indicate nutrient contributions from the nearby urbanized shoreline. In contrast, and more similar to patterns observed in lower nutrient regimes, epiphytes at the deep RIV station during the winter dry season were greater than the shallow station loads. Shallow to deep differences in epiphytic loads were less prominent at the remaining stations.

Total Attenuation

The percentage of PAR reduction produced by epiphytic cover is substantial and should be considered when examining light requirements for seagrasses which exist across a variety of nutrient regimes. The percentages of PAR remaining in the water column at the maximum depth limits were accordingly further reduced by the percentage attenuation of the epiphytic load. Mean percentages by month and year were computed analogously to the water column percentages described above, and appear in Table 8. The **PAR available to the seagrass (% PAR_t) is more nearly represented by the adjusted percentages, but % PAR, is an incomplete and inappropriate water column clarity target if any epiphytic cover is present.**

Among the four stations, the PAR received through the water column **and** epiphytic cover amounted to between 13.0% and 14.2% of subsurface irradiance on an annual basis, and between 10.8% and 13.8% during the growing season. Station comparisons were performed with Friedman's ANOVA and indicated that while PIN and PRT were similar, and PRT and RIV not significantly different, other station combinations were all significantly different ($p < 0.05$). The % PAR, were converted to total attenuation coefficients (using the station depths) and appear against maximum depth limits of the four stations in Figure 27. It is apparent that including the effects of epiphytes significantly improves the strength of the regression of K_0 against maximum depths. Water column attenuation coefficients are grouped around the 22.5 % isolume, while the

total attenuation coefficients (of water column and epiphytes) are more tightly clustered around the 13.8 % isolume. In fact, the regression of total attenuation coefficient against maximum depth achieves a significance of $p < 0.05$. When the growing season (May-September) alone is examined, total K_0 again exhibits a stronger relationship than the water column K_0 alone and is significant at the $p < 0.10$ level.

PAR climate data available from the maximum depths of *Thalassia* and *Halodule* beds in Sarasota Bay were also examined and compared with the Tampa Bay results (Figure 28). Data plotted from both studies are maximum depths against total (water plus epiphytes) attenuation coefficients. For Sarasota Bay, the level of epiphyte attenuation was determined monthly rather than bimonthly as for Tampa Bay. The PAR available to the *Thalassia* blades (after water column and epiphytic attenuation, % PAR_a) at both locations fall within isolines ranging from 13% to 24% of subsurface scalar irradiance. The greater scatter in the Sarasota Bay data may be explained by the fact that the annual percentages are derived from bi-weekly rather than continuous data. In addition, Sarasota Bay data were from both *Thalassia* and *Halodule* beds, although the grouping between the three *Thalassia* stations was excellent, with blades at the three beds receiving 22%, 23%, and 24% as an annual average.

Annual Light Regimes

Annual PAR received both at maximum depths and by the *Thalassia* blades was computed by summing the PAR values from the bottom sensor, both as measured and after reduction by epiphytic attenuation. Monthly totals and daily averages appear in Tables 9 and 10 and daily averages received by month by *Thalassia* blades are illustrated in Figure 29. The RIV site apparently, through a combination of water clarity and low epiphytic load, received much higher daily PAR totals than other stations during April and May. The low epiphyte load at the RIV site offset the high water column attenuation values noted there during the fall, such that average $E \text{ m}^{-2} \text{ day}^{-1}$ received at the RIV site was very similar to other stations. Also noteworthy is the consistently low levels of PAR received at the deep edge of the PIN site. Monthly averages of daily totals at PIN never exceeded $10 E \text{ m}^{-2} \text{ day}^{-1}$. Long term reductions in PAR to below $5 E \text{ m}^{-2} \text{ day}^{-1}$ have been linked to reduction in biomass and disappearance of *Halodule* from maximum depths in Texas (Dunton, 1994).

Annual totals of PAR in the water column and after epiphytic attenuation appear in Table 11. While many station to station differences were significant for both water column attenuation coefficient and percentage of PAR available to *Thalassia*, it is striking that the range of PAR received annually by three of the four stations is so small. Water column levels ranged between $4,800$ and $4,900 E \text{ m}^{-2} \text{ year}^{-1}$ for MUL, PRT, and RIV, while PIN received $3,600 E \text{ m}^{-2} \text{ year}^{-1}$. PAR totals received by the blades ranged between $3,000$ and $3,100 E \text{ m}^{-2} \text{ year}^{-1}$ for MUL, PRT, and RIV, while PIN received $2,200 E \text{ m}^{-2} \text{ year}^{-1}$. The PIN site was also distinguished by the higher above-to below-ground biomass ratios (lower root:shoot ratios) observed at both shallow and deep

stations, a characteristic which has been linked with reductions in light intensity (Kemp et al., 1988; Dunton, 1994) and by a reduction in shoot density between the beginning and end of the project.

In addition, the plastochrone interval determined at the various stations indicated that among the deep stations the number of blades produced was lowest at PIN, 6.6 blades year⁻¹, compared with 8.1, 9.2, and 9.9 blades year⁻¹ at MUL, PRT, and RIV, respectively.

Similarity of MML and Other Monitoring Programs

The correspondence of the continuous data generated by MML with data from less frequent sampling programs was examined. The data from the 1994 HCEPC sampling program were initially transformed from Secchi depths to estimated attenuation coefficients using the generalized relationship (Giesen *et al.*, 1990):

$$k_0 = \frac{1.65}{\text{secchi (m)}}$$

Raw monthly data ($n = 1$) from the HCEPC stations nearest to the continuous light sites were superimposed on the monthly means and standard deviations of K_d calculated at the MML sites for the 1000-1400 hours period (Figure 30). The general seasonal correspondence between data sets is good, and HCEPC data typically fell within the envelope of the MML observed mean \pm sd. The most evident deviation was for the RIV site, in which instance the nearest HCEPC station is some distance away from the mouth of the Manatee River, and is clearly more influenced by Gulf waters rather than the freshwater from the Manatee River.

Even where HCEPC and MML sites were in close proximity, however (MUL and HCEPC-96) a consistent bias was observed, which could result in a difference of 6% in the annual light percentages calculated. Measurements of K_0 during MML fieldwork detected significant differences between the shallow and deep station pairs at PIN and the conclusion is that circulation patterns, fetch, and wave action may produce significant micro-scale variations in water clarity. This is also evident in Figure 31, where monthly mean attenuation coefficients (1000-1400 hours) from MML sites are compared with the envelope of Secchi-derived HCEPC data (monthly means \pm sd) from HCEPC Stations 19, 21, 23, 24, 25, 28, 90, 91, 92, 95, and 96, or those stations in the lower Middle and Lower Tampa Bay segments.

Correspondence between MML and HCEPC data is good for the winter months when water clarity is high, despite the presumption that intermittent sampling will underestimate water clarity due to not sampling storm events. With increasing attenuation during summer and fall, however, when the influences of color and

chlorophyll on water quality increase, the network of HCEPC stations do not represent the nearshore locations as well. As a result, the HCEPC and COT sampling program, while a useful first order approximation to extend the results of the light requirements project to the remainder of Tampa Bay, may not always adequately simulate nearshore water clarity.

Extension of Light Requirements to the Remainder of Tampa Bay

Data from the 1994 monitoring programs of the City of Tampa and the Hillsborough County Environmental Protection Commission were used to estimate water clarity at a number of locations and to determine the average depth to which sufficient light for *Thalassia* penetrated. Station water clarity was evaluated under both "heavy" and "moderate" epiphyte conditions. An important assumption implicit in the calculations is that epiphytic loads and subsequent attenuation were comparable (or estimable) in the other regions of the Bay. Other assumptions made were that nearshore environments were accurately represented and that an intermittent sampling program accurately approximated continuous conditions.

The larger portion of water clarity data for Tampa Bay exists as Secchi depths collected by the HCEPC, but the coverage afforded by both HCEPC and COT is quite dense (totaling 64 stations) and extends from upper Hillsborough and McKay Bay to offshore from Egmont Key (Figure 32). Previous researchers have developed empirical relationships between attenuation coefficient and secchi depths (Giesen *et al.*, 1990; Batiuk *et al.*, 1992). Conversions ranging from $K_d = 1.7 \bullet (\text{Secchi, m})^{-1}$ to $1.44 \bullet (\text{Secchi, m})^{-1}$ have been proposed, with $K_d = 1.65 \bullet (\text{Secchi, m})^{-1}$ the average of a large number of studies (Giesen *et al.*, 1990). A conversion of $K_d = 1.44 \bullet (\text{Secchi, m})^{-1}$, presented as more appropriate for turbid waters (Holmes, 1970), was used by King Engineering Assoc. (1992) in the review of Tampa Bay historical water quality data and empirical regression analyses of factors contributing to attenuation. Janicki and Wade (1994), however, employed segment-specific conversion factors developed from the simultaneous Secchi depth and attenuation coefficient data collected by COT. The segment-specific conversions used to convert the 1994 HCEPC data were provided by the COT (R. Johansson, personal communication), were based on data from 1989-1994, and appear below, while COT scalar attenuation coefficients were used directly.

Hillsborough Bay	$K_0 = 1.61 \bullet (\text{secchi, m})^{-1}$
Old Tampa Bay	$K_0 = 1.49 \bullet (\text{secchi, m})^{-1}$
Middle Tampa Bay	$K_0 = 1.84 \bullet (\text{secchi, m})^{-1}$
Lower Tampa Bay	$K_0 = 1.63 \bullet (\text{secchi, m})^{-1}$

From computed and observed attenuation coefficients, data were transformed to the percentage of subsurface PAR at segment-specific target depths for each individual reading and averaged over the year and over the growing season (May-September) by station. Target depths used were 1.34 m, 1.84 m, 1.84 m, and 2.34 m mean water column depths for Hillsborough, Old Tampa, Middle Tampa, and Lower Tampa Bays, respectively, corresponding to the 1.0 m, 1.5 m, 1.5 m, and 2.0 m (MLLW) target depths established for the various segments (Janicki *et al.*, 1994). (Mean tide level is approximately 0.34 m higher than MLLW for stations in Tampa Bay [U.S. Department of Commerce, 1994]). Target depths are conservative estimates which were selected to include 95% of the maximum depth limits of seagrasses in the 1950's (Coastal Environmental, 1995).

Mean station PAR percentages at target depths for both annual and growing season periods appear in Tables 13 and 14 grouped by Bay segment. From target depths and percentages, annual average K_0 values are recomputed in order to calculate the depths to which the annual and growing season light requirements extend and to assess whether targets are currently being met. For Table 13, the initial maximum depth is based on an annual water column light requirement of 22.5%, and an average epiphytic attenuation of 38.7%, for a plant requirement of 13.8% of subsurface irradiance, as determined in Lower Tampa Bay by this project.

As gradients in both nutrient loads (Zarbock *et al.*, 1993) and in water column nutrients (HCEPC, 1989; King Engineering Assoc., 1992) clearly exist in Tampa Bay, epiphytic cover (and attenuation) is expected to be greater in the higher nutrient regimes of the upper portions of the Bay. Accordingly, water clarity measured in the upper Bay segments was also evaluated using the higher epiphytic attenuations measured in Sarasota Bay (Table 12), as being potentially more representative of a higher nutrient environment.

Epiphytic attenuation from a roughly equivalent time period in Sarasota Bay was used to recompute the water column light requirements, by keeping the plant requirement fixed at 13.8 %. At an annual epiphytic attenuation of 50%, for example, water column PAR percentages must exceed 27.5% to provide the required 13.8% PAR to the *Thalassia* blades. The increased epiphytic load is not calculated for Lower Tampa Bay stations, as the epiphytic load determined during the project is considered representative of this segment. Analogous calculations appear in Table 14 for the growing season alone.

Results indicate that 40% of the HCEPC and COT stations in Hillsborough Bay have annual average water clarity which could support *Thalassia* to target depths, while 50% of stations in Old Tampa Bay have adequate PAR at depth. Of all the stations in Middle and Lower Tampa Bays, 36% and 58%, respectively, have adequate light at the segment-specific target depths. The percentages of acceptable stations are determined under the epiphyte loadings and attenuation conditions as measured for Lower Tampa Bay.

Evaluation of the stations under higher epiphyte attenuations necessarily reduces the number of stations which would have adequate light at the target depths. Figure 33 illustrates the stations which meet segment-specific target depths for both low and high epiphyte levels, while Figure 34 illustrates the stations meeting water clarity requirements at target depths during the growing season alone.

Unfortunately, examination of annual average water clarity ignores the potential controlling functions of episodic events of lowered water clarity. Additionally, evaluation of stations for light requirements alone ignores other physiological requirements of *Thalassia*. Some stations in the head of Hillsborough Bay and in McKay Bay have unsuitable salinity regimes for *Thalassia* and it is unlikely that the species was ever present in large areas or over long periods of time. Accordingly, it should be emphasized that the suitability of stations for *Thalassia* at target depths, as listed in Tables 13 and 14, is an approximation only and only addresses annual average light requirements.

The distribution of stations which fail to meet water clarity targets, in general, parallels the distribution of areas where large expanses of seagrass have been lost since the 1950's (Janicki *et al.*, 1994; Appendix A). Lower Tampa Bay has few areas marked as restoration targets, and comparatively few stations which fail to meet water clarity requirements at the target depths. For Middle Tampa Bay, the northeastern edges, from the mouth of the Little Manatee River and into Hillsborough Bay as well as the southeastern portion of the mid-Bay peninsula have stations with water clarity below required amounts at target depths. Similarly, most of Hillsborough Bay and the northern and western portions of Old Tampa Bay are distinguished both by large areas of seagrass lost and by stations at which required PAR percentages do not extend to target depths.

Discrepancies between stations which appear to have adequate light and yet seagrass loss has been identified (the mouths of Old Tampa Bay and Hillsborough Bay, for example) may be the result of the lack of suitability of the assumptions in the analysis. Other physiological needs (salinity) may not be met. Epiphytic loads may exceed 50% attenuation or blooms of drift algal species may periodically completely cover available seagrass habitat. Nearshore environments may be more or less turbid from wave action or circulation patterns. Other researchers report areas of higher water clarity nearshore in Hillsborough Bay (R. Johannson, personal communication). Long term patterns of water clarity (King Engineering Assoc., 1992) illustrate the frequent seasonal appearance of an area of less turbid water which extends up the middle of Tampa Bay, further evidence of water clarity differences between mid-Bay and nearshore environments.

Halodule wrightii

The lack of depth limited *Halodule* beds near the continuous light monitors prevented the direct estimation of PAR requirements for this species during the study. Patterns of occurrence throughout the Bay, where *Halodule* typically dominates the shallow intertidal

zones when assemblages of mixed grasses appear (Phillips, 1960; Lewis *et al.* 1985), may indicate that other species have a competitive advantage at comparable PAR levels. *Halodule*, however, more tolerant to exposure and desiccation, can exist in intertidal regions. The advantage at depth may be something as direct as blade length and the amount of PAR that a blade can “capture” when in a canopy of mixed species, or may relate to photosynthetic efficiency, patterns of resource allocation, sediment requirements, or other physiological differences.

If *Halodule* is out-competed at depth, then the issue of light requirements for the species, becomes pertinent only for regions in which other seagrass species do not generally exist (*i.e.*, Hillsborough Bay). To determine the suitability of Hillsborough Bay for *Halodule*, light requirements developed elsewhere can in theory be applied to the observed water column conditions. A severe limitation to the extrapolation of data from other areas, however, is that the PAR attenuation provided by the epiphytic community is generally undescribed in those works which detail PAR requirements for *Halodule*. Comparison of photosynthetic parameters (E_k , E_{c-leaf}) between the species may be instructive, but whole plant determinations of carbon budgets depend on detailed seasonal information on tissue apportionment, respiration and photosynthetic rates.

Nearby work in Sarasota Bay (Dixon and Kirkpatrick, 1995) illustrated that epiphytic attenuation for *Halodule* can range between 13% and 99% over the course of a year, and that annual averages at individual stations ranged between 44% and 56%. The nutrient (nitrogen) loadings to Sarasota Bay range between 20 and 200 metric tons year⁻¹ (CDM, 1992) are substantially lower than the 1000 metric tons year⁻¹ described by Johansson (1991) for Hillsborough Bay. As epiphytic growth responds directly to increases in nutrients (Tomasko and Lapointe, 1991; Dunton, 1990; Borum, 1985), the potential is high for very heavy growths of epiphytic communities in Hillsborough Bay. As a result, values of PAR requirements for *Halodule* determined elsewhere should be considered as a minimum value, unless specific information is available on the nutrient regime, or epiphytic cover.

Annual percentages of PAR present in the water column at depth limited *Halodule* stations in Sarasota Bay (Dixon and Kirkpatrick, 1995) ranged between 28% and 50% of subsurface scalar irradiance. Attenuation by epiphytes reduced these annual percentages to between 12% and 22% actually received by the *Halodule* blades. (It is unknown whether any changes in areal seagrass coverage occurred during this study as no measurements of shoot density, biomass, or condition were performed.) Once the attenuating effects of epiphytes were considered, however, there were no species-specific consistent differences in PAR levels noted between *Halodule* and *Thalassia* stations. The range of 12-22% noted for Sarasota Bay *Halodule* is also not substantially different from the 13-14 % received annually by *Thalassia* in Tampa Bay (after both water column and epiphytic attenuation are considered), and indeed agreement between Tampa and Sarasota Bay stations for maximum depths as a function of total (water column plus epiphytes) attenuation is quite good (Figure 28 above).

An interesting difference noted in the Sarasota Bay data between *Thalassia* and *Halodule* annual light climates was that *Halodule* appears able to tolerate extended periods of very low total PAR (Figure 35). Many monthly means (of biweekly data) of PAR available to the plant were below 10% of subsurface scalar PAR. *Thalassia*, on the other hand, existed under a relatively more uniform light climate over the year when the effects of both water column and epiphytic attenuation were included. Both species, however, received approximately 20% of subsurface PAR during the growing season, or slightly higher than the 13-14% levels noted during the present study. Kenworthy (1993) also speculated that *Halodule* could take advantage of relatively short optimal growing conditions.

Other data bases on PAR requirements specific for *Halodule* include Kenworthy (1993), developed for both *Halodule* and *Syringodium filiforme* (which grew to comparable depths) in Hobe Sound on the east coast of Florida. From long term records of attenuation coefficients, PAR levels **in the water column** at seagrass depth limits in the Lagoon range between 27% and 37%) with the higher value recorded at the location farthest from the inlet. As exchange with oceanic water is least at this location, values of water column nutrients and epiphytic growth may account for the variation in water column PAR requirements, but direct information on epiphyte attenuation was not a part of this work.

More recently, Dunton (1994) provided extensive and continuous PAR data specific for *Halodule* in Texas. Two of the three sites were at the reported depth maxima for the species in the area. The data indicated that a range of $2100\text{-}2400 \text{ E m}^{-2} \text{ year}^{-1}$ was required to maintain *Halodule* with minimal epiphyte growth, that $2300 \text{ E m}^{-2} \text{ year}^{-1}$ resulted in the complete loss of the plants under conditions of heavier epiphyte growth, and that $3300 \text{ E m}^{-2} \text{ year}^{-1}$ maintained the deep edge of *Halodule* under unspecified epiphyte cover-ages. Epiphytic attenuation, however, was not quantified directly.

Dunton's (1994) values for *Halodule* can be contrasted to the Tampa Bay water column data of $4900 \text{ E m}^{-2} \text{ year}^{-1}$ to maintain the deep edge, and low light stress at $3600 \text{ E m}^{-2} \text{ year}^{-1}$. Other comparisons can be made between Dunton's (1994) low epiphyte requirements of $2100\text{-}2400 \text{ E m}^{-2} \text{ year}^{-1}$ and the plant available PAR determined in Tampa Bay of $3100 \text{ E m}^{-2} \text{ year}^{-1}$ to maintain the deep edge, with low light stress at $2200 \text{ E m}^{-2} \text{ year}^{-1}$. These data indicate that *Thalassia* and *Halodule* annual PAR requirements may be very similar.

In contrast, photosynthetic parameters (E_c and E_k) available for both *Halodule* and *Thalassia* (Fourqurean and Zieman, 1991a, 1991b; Dawes and Tomasko, 1988; Tomasko and Dunton, 1991; Dunton and Tomasko, 1991, 1994; Williams and McRoy, 1982) indicate that compensation irradiance for *Halodule* may be higher than for *Thalassia*. It is difficult, however, to apply laboratory determinations reliably on leaf sections to in situ conditions and predict depth limits or production for *Halodule* (Dunton and Tomasko, 1994). The wide range in photosynthetic parameters observed can also be

attributed to methodological differences, primarily angle of incident irradiance (Dunton and Tomasko, 1994). Photosynthetic parameters are more readily available for leaf tissue alone, but the varying amounts of below-ground tissue and associated respiratory demands can drastically alter predicted carbon budgets.

Compensation points ($E_{c\text{-plant}}$) reported for whole plants *in situ* include values of $85 \mu\text{E m}^{-2} \text{ sec}^{-1}$ (scalar, E_0) for *Halodule* (Dunton and Tomasko, 1994), although the absolute values increased substantially with increasing root:shoot ratios. Fourqurean and Zieman (1991b) reported $40 \mu\text{E m}^{-2} \text{ sec}^{-1}$ for *Thalassia* and $65 \mu\text{E m}^{-2} \text{ sec}^{-1}$ for *Halodule* (as downwelling light, E_d), indicating higher light requirements for *Halodule*. Variation in the $E_{c\text{-plant}}$ determined for *Thalassia*, however, ranged between 25 and $85 \mu\text{E m}^{-2} \text{ sec}^{-1}$, a result of varying percentages of below-ground biomass. The demonstrated seasonal variations in respiration (Dunton and Tomasko, 1994; Dennison, 1987), P/E parameters (Tomasko and Dawes, 1990), and tissue apportionment Dawes and Lawrence, 1980), and the lack of specific information on these variables for Tampa Bay Halodule, make the estimations of light requirements from literature values of photosynthetic parameters problematic. Additionally, the magnitude of PAR attenuation that epiphytic communities can achieve adds a further uncertainty to any estimate that cannot be overcome without site-specific epiphyte attenuation data.

A conservative approach (from the standpoint of requiring additional nutrient load reductions) was employed above in evaluating which Tampa Bay stations met seagrass restoration targets. The effects of a range of epiphytic cover was evaluated by applying both the relatively low epiphytic attenuation measured in Lower Tampa Bay and the higher values measured for Sarasota Bay. The higher nutrient loading to Hillsborough Bay, from non-point source, point source, and industrial discharges, is expected to result in higher epiphytic loads than measured for Lower Tampa Bay and so the assessment of whether stations meet *Thalassia* PAR requirements is probably overoptimistic, even using the Sarasota Bay epiphytic attenuation percentages.

For *Halodule*, assessment of whether water quality at monitoring stations meets water clarity requirements for seagrasses is difficult, given the conflicts between annual light requirements (comparable requirements for both species) and critical light values (higher compensation point for *Halodule*). Seasonal PAR levels may also be important in controlling depth distributions. In view of the uncertainties, and in the absence of actual data on the epiphytic loads of seagrasses in Hillsborough Bay, no further approximations appear appropriate at this time.

Seagrass Biomass and Growth Parameters

To place the various biological measurements (above-ground growth, biomass, chlorophyll, and production) in context, light regimes recorded at each site during the period between marking and recovery of blades were provided in detail, as well as a nearby record of incident irradiance (Figures 14-18). Storm effects on both incident and

subsurface irradiance and attenuation coefficients are clear. Other light related parameters to keep in mind are the seasonal patterns of water clarity (decreasing in the summer months) and epiphytic attenuation.

The biological parameters included both descriptors of biomass, proportions of above- and below-ground tissues, mean blade length, leaf area per shoot, leaf area index, and shoot density. Growth parameters evaluated included leaf relative growth rates, production per shoot and production per unit area. Epiphytic biomass was examined, and from photosynthesis-irradiance measurements provided by Dr. Dawes, coarse estimates of daily light periods provided. Statistical testing results (Appendix B) and data summaries (Appendix C) are included.

Shoot Density

Thalassia shoot densities for shallow and deep stations at each site are summarized in Figure 36. Shoot densities at shallow stations were three to six times higher than at their deep station counterparts. Shallow station shoot densities were in the range of 200-350 shoots m^{-2} , while deep station densities varied between 50-100 shoots m^{-2} . Not surprisingly, mean shoot density was significantly different ($p < 0.001$) between shallow and deep stations at all sites for each period. This pattern is consistent with that found by numerous researchers, and for many species besides *Thalassia* (Hall *et al.*, 1991; Kemp *et al.*, 1988; Tomasko and Dawes, 1990; Dawes and Tomasko, 1988). Indeed, the exponential decrease in density and biomass with depth is one of the major pieces of inferential evidence supporting the concept of light limitation of submerged macrophytes (Duarte, 1991). One distinct competitive advantage of lower shoot densities at the deep edge is that a larger area of blade surface area can be exposed to available PAR.

Overall, *Thalassia* shoot densities observed were somewhat lower than shoot densities reported from similar depths along the west Central Florida coast. Dawes and Tomasko (1988) reported 454 and 284 shoots m^{-2} at shallow and deep stations, respectively, from Anclote Key during summer. At Mullet Key, Tomasko and Dawes (1990) found 511 and 152 shoots m^{-2} at shallow and deep stations, respectively, from June through November. Hall *et al.* (1991), at an almost identical location to the MUL site, found peak shoot densities of near 550 shoots m^{-2} and 250-300 shoots m^{-2} for shallow and deep stations, respectively. The lower shoot densities found at the deep stations of this study are attributed to station selection, in which the very edge of a light-limited bed was sampled. Discussions above have demonstrated the rapid increase in shoot density with distance from the edge of the bed, and the distance of a few meters could readily account for the magnitude of the apparent difference. No obvious reason for the lower densities at the shallow sites was apparent.

Shoot densities at shallow stations varied considerably, both temporally and spatially, while deep station shoot densities were more consistent. The shallow stations at RIV and PIN exhibited some seasonality in shoot density, with increased densities during the April

and May. At MUL, reductions in shoot density in June may indicate thermal stress, although counts rebounded by August when water temperatures were still high. Shallow station shoot density was typically lowest at PIN. Overall shallow station densities were generally as follows: MUL, 250-350 shoots m^{-2} ; PIN, 150-250 shoots m^{-2} ; PRT, 200-300 shoots m^{-2} ; and RIV (250-400 shoots m^{-2}). Shoot densities at deep stations typically ranged between 50-100 shoots m^{-2} with differences between season or station much less apparent than for shallow stations.

Biomass and Tissue Percentages

Above-ground biomass (gdwt m^{-2}) over time for each site is shown in Figure 37. Similar to expected and observed patterns in shoot density with depth, above-ground biomass was significantly higher (*t*-test, $p < 0.05$) at shallow stations throughout the study, except at PIN during August, when decreases in biomass at the shallow station approached the levels observed at depth. During June and continuing through October, the difference in biomass between deep and shallow stations at PIN and MUL were also minimal.

PIN-D displayed the highest above-ground biomass among the four deep stations, while RIV-S generally had higher above-ground biomass than the remaining shallow stations. Above-ground biomass was highest during April or June, and seasonal patterns in biomass were particularly pronounced at the RIV shallow station. Seasonal variations in biomass at deep stations was present but minimal in contrast to that observed at the shallow stations. Biomass in October had generally returned to the levels observed during the initial December sampling.

Comparisons in above-ground biomass among shallow and deep stations at all sites are shown in Figure 38 in a format better suited to discerning inter-station, as opposed to seasonal, differences.

In addition to displaying greater seasonal responses, biomass at shallow sites exhibited a wider range of values during any one time period. The dramatic seasonal increases at some shallow sites (RIV) reflect not only an increase in shoot density, but also high values of leaf area per shoot (see below). Overall deep stations exhibited fewer significant differences between stations at any one time. The significantly ($p < 0.05$) lowered biomass at MUL-D in February may be linked to the heavy cover of drift algae observed during this sampling, while the lower biomass at RIV-D could have been caused by exfoliation due to low salinity stress.

Thalassia biomass data were also analyzed according to the proportions of three major tissue components; blades, short shoots, and combined roots and rhizomes. Additionally, *Thalassia* biomass was divided into an above-ground portion consisting of blades, and a below-ground portion of short shoots and roots and rhizomes for calculations of above to below-ground (A:B) ratios of tissue weights. Results are presented by quarterly sampling, December, April, August, and October, in Figures 39 through 42.

Averages of tissue percentages were 23%, 37%, and 40% for blades, shoots, and combined roots and rhizomes, respectively, although the ranges both within seasons and within stations was considerable. At stations other than PIN-D, blade tissue constituted nearly 20% of the total biomass during January, August and October, increasing in April to approximately 35% with the increase in above-ground biomass. The effects of higher apportionment of seagrass biomass to the leaves with respect to changes in whole plant compensation irradiance is discussed below.

During April, overall percent blade biomass was greater than for any other time and reflected the seasonal increase in above-ground biomass observed during this period. As a result, percent root biomass was slightly lower, reduced to 33%. Percent blade biomass in August was similar among all stations (15-20%) except PIN-D, where it comprised 35% of the total biomass. High variability in shoot and root and rhizome percents was also noted for this sampling.

The relative contribution of blade tissue to total biomass decreased slightly during October with decreasing above-ground biomass values. Seasonal patterns of root-rhizome percents was generally the inverse of that observed for blade percentages. RIV-D generally had a higher percent root and rhizome biomass than any other station, due to low above-ground biomass totals. Other stations with high values of root-rhizome percents included MUL-S and MUL-D.

Overall, PIN-D stands alone in having a higher percentage of its biomass allocated to blade material during all samplings and particularly during May. To some extent, this is a product of both the longer mean blade lengths observed at the station, and also in the higher values of leaf area per shoot (see below). Examination of raw weights, however, also indicated that rhizome tissues were substantially lower at PIN-D and at PIN-S than at the other stations of comparable depths. Average dry weights of rhizome per core were 0.8 g at PIN-D, in contrast to between 1.4 to 1.9 g at other deep stations. Weights of rhizome tissue per shoot were also approximately half the values at other stations.

Leaf scar and shoot length were examined. Scars per cm of shoot length averaged between 11 and 13 scars cm^{-1} for all deep stations except PIN, which averaged near 7 scars cm^{-1} . Currents were notable at the PIN station and it is possible that accretion of sand on the shoal near Pinellas Point is covering the base of the shoots, forcing an accelerated vertical growth, with the result that “basement” rhizome layers were below the reach of the coring device. Alternatively, lower levels of PAR noted at PIN may have resulted in the mean blade elongation, and an increase in A:B ratios (decrease in root:shoot ratio) similar to the light stress evidenced by *Halodule* (Dunton, 1994). Potential light stress at this site is consistent with the lower annual PAR received at depth (in comparison to other stations) and the observed decrease in shoot density between initial and final samplings.

Ratios of above- to below-ground biomass were remarkably consistent for all stations, again with the exception of PIN-D and, to a lesser extent, PIN-S. Averages over the project were near 0.2 with otherwise little variation noted between sites or deep and shallow stations. During April, when above-ground biomass was greatest, A:B ratios averaged 1.5 for PIN-D.

The majority of *Thalassia* biomass is below the sediment surface, with only 15-20% in the leaves (Zieman and Zieman, 1989), although the distribution varies seasonally (Fourqurean and Zieman, 1991a). An increase in the percent leaf biomass in the current study was observed in May. Leaf biomass of *Thalassia* reaches a seasonal maximum during the summer (Iverson and Bittaker, 1986; Zieman, 1974). The extent of variability in the seasonal response of seagrass biomass is constrained by the latitudinal location of the seagrass meadow, those at lower latitudes sustain a more uniform biomass throughout the year (Duarte, 1989). The effect of variation in the relative importance of leaf biomass to E_c of the whole plant can be substantial.

The relationship between above- to below-ground biomass ratios and depth remains unclear. While Dawes and Tomasko (1988) reported higher ratios at the deep edge of *Thalassia* meadows at Anclote Key, they found the reverse pattern from the deep edge off Egmont Key, and speculated that the site was not light-limited. An increase in the ratio of *Thalassia* above- to below-ground biomass with depth has been reported from coastal Caribbean meadows (Buesa, 1975; Kemp *et al.*, 1988), while Dunton (1994) reports an increase in A:B ratio under low light stress for *Halodule*. In the present study, a consistent trend with depth was not observed, and the conditions at PIN-D may indicate the early responses to low light stress.

Finally, the A:B biomass ratios calculated from this study were consistently lower than those reported by Dawes and Tomasko (1988) despite the fact that a 30 cm corer was used in their work (compared to a 20 cm device for this project). Project values of near 0.2 however, are very comparable to the ratio of 0.17 derived from tissue proportions given in Fourqurean and Zieman (1991a). This may be a result of a varying definition of below-ground biomass, which for this work we defined as including roots, rhizomes, and shoots.

Mean Blade Length

Mean blade length per shoot data for each site are presented in Figure 43. At all sites (except PIN-D), blade length increased from December through June, then decreased through October. Lengths in October were still longer at all stations than during the initial December sampling, despite the exfoliation noted at the RIV-D site. At PIN-D, blade length increased through August and remained high through October. Unlike other stations, total PAR received by blades at PIN-D had been low (near $5 \text{ E m}^{-2} \text{ day}^{-1}$ average) for several months prior to the August sampling.

During the winter months, mean blade lengths averaged near 10 cm, increasing to between 20 and 30 cm by June and August. Mean blade length of the deep stations (again with the exception of PIN) was generally either comparable to or longer than the lengths at shallow stations. The differences between deep and shallow were minimal at MUL, moderate at RIV, and more pronounced at PRT. At PIN, blade lengths were usually longer at the deep station.

Mean blade length comparisons among shallow and deep stations at all sites are shown in Figure 44. At the deep stations, PIN consistently exhibited significantly longer ($p < 0.05$) blades than other stations, most notably RIV and MUL. PRT-S displayed significantly longer ($p < 0.05$) blades than other stations during April and June. Increased blade lengths are one of the typical morphological responses, produced by shading (Goldsborough and Kemp, 1990).

Leaf Area Per Shoot

Leaf area per shoot data, which represent a summation of the changes in leaf length, width and blade number, are presented for each site in Figure 45. Leaf area per shoot values exhibited a marked seasonality at all sites. Again with the exception of PIN-D, leaf area was highest during April and June and exceeded 75 cm^2 at both PRT and RIV shallow stations during this period. At PIN-D, the maximum leaf area were also above 75 cm^2 but, but similarly to mean blade lengths, the maximum value was not observed until August. This again may indicate a response to lowered light levels. Leaf area per shoot values were usually lowest during December and February (near $10\text{-}20 \text{ cm}^2$) with the exception of the RIV-D station in October, which again exhibited the effects of exfoliation from lowered salinity stress.

From April through October, shallow stations at PRT and RIV exhibited higher leaf areas than their respective deep stations, while the deep station at PIN had a higher leaf area than the shallow station. Comparisons of leaf area per shoot among shallow and deep stations at all sites are shown in Figure 46. Among shallow stations, RIV displayed significantly higher ($p < 0.05$) leaf area per shoot during December and February. Among deep stations, PIN had the greatest leaf area per shoot from June through October.

Leaf area per shoot integrates changes in leaf length, width, and blade number that may occur in response to reduced light (Hall *et al.*, 1991). Leaf area of *Thalassia* might be expected to increase with a decrease in light quantity. This response was not observed with respect to the shallow and deep stations in the present study. Shallow stations typically had slightly higher leaf area per shoot than deep stations, similar to the interdepth comparisons of blade lengths. Leaf area per shoot at PIN-D, however, was higher than at PIN-S from April through Oct., and higher than all other shallow stations during both August and October. These differences are the result of the higher mean blade length at shallow stations (deep station at PIN). Hall *et al.* (1991) found a short

term increase in leaf area in *Thalassia* that had been shaded to reduce available light. However, by nine months post-shading, leaf area per shoot was higher in controls than shaded plots at both deep and shallow stations. The increased blade area per shoot at PIN-D could represent an early morphological change to decreases in PAR.

Leaf Area Index

Leaf area indices (LAI) for each site are presented in Figure 47. Leaf area index incorporates changes in both leaf area and shoot density. Once again, this parameter displayed conspicuous seasonality at all sites. Low leaf area indices occurred during December and February, when mean blade length and to less extent shoot density were low. High leaf area indices were found during April and June, with the higher values observed in April.

Highest leaf area indices were found at RIV-S and PRT-S. Leaf area indices were significantly different ($p < 0.05$) between shallow and deep stations at all sites during the study, primarily reflecting the shallow to deep differences in shoot density. Values at deep stations were typically $0.5 \text{ m}^2 \text{ m}^{-2}$ or less, while at shallow stations LAI was generally closer to $1.0 \text{ m}^2 \text{ m}^{-2}$, and extending as high as $3.3 \text{ m}^2 \text{ m}^{-2}$. Differences in LAI between shallow and deep stations were greater at RIV and PRT and less pronounced at MUL and PIN, especially during the summer months.

Comparisons of leaf area indices among shallow and deep stations at all sites are shown in Figure 48. Among shallow stations, MUL and RIV were significantly different ($p < 0.05$) than PIN and PRT during December and February. During June, PRT and RIV were significantly different ($p < 0.05$) than MUL and PIN. Leaf area index among deep stations were similar throughout the year. The increased blade length and blade area per shoot produced an increase in LAI at PIN-D during August.

Leaf area index (LAI) takes into account changes in both leaf area and shoot density which may occur with light reduction. LAI was much higher at shallow stations than at deep stations, reflecting the higher shoot densities at shallow stations. While increased leaf area indices may provide shallow plants an advantage of more light absorption surface, the effects of self-shading (due to higher shoot densities) make high LAI structures less adaptive under extreme shading (Kemp *et al.*, 1988).

Leaf Relative Growth Rate

Leaf relative growth rates, defined as new blade material per total blade weight per day, are shown for each site in Figure 49 and were typically between $15\text{-}35 \text{ mg gdwt}^{-1} \text{ day}^{-1}$. As for above-ground biomass, blade lengths, and blade area per shoot, pronounced seasonality was evident in this parameter. Growth rates during December were greatly reduced compared to the rest of the year. Highest growth rates were observed during

April and June at all sites. Flowering was observed in the *Thalassia* at RIV-S during the April sampling.

Comparisons of leaf relative growth rates among shallow and deep stations (Figure 50) illustrate no consistent depth-related differences throughout the year. Rates of 27-35 mg gdwt⁻¹ day⁻¹ during June were quite comparable to the rates of 21-31 mg gdwt⁻¹ day⁻¹ determined by Dawes and Tomasko (1988), who also discerned no consistent pattern of growth with depth. The results for LRGR were in concert with Hall *et al.* (1991) who found no differences between shallow and deep control locations although LRGR might be expected to decline with decreasing light (Hall *et al.*, 1991). Tomasko and Dawes (1990), however, showed higher LRGR in deep *Thalassia* ramets compared to shallow ones.

Above-ground Growth

Above-ground growth or blade production is defined as the weight of new blade per shoot per day (mg shoot⁻¹ day⁻¹) and results for each site are displayed in Figure 51. Seasonal variation dominates and there are no consistent variations with depth. Above-ground growth was very low during December and February at all sites. By April, above-ground growth had increased to the highest rates achieved during the study, gradually decreased in June, and remained relatively constant and low in August and October at all sites. Above-ground growth showed no consistent trends between stations or with depth (Figure 52), although for shallow stations, it was generally higher at PRT and RIV, and higher at the deep station at PIN. Higher shoot relative growth observed at PIN-D is consistent with the increased biomass, increased blade lengths, and leaf area per shoot already noted for this station.

Blade production values of approximately 7-13 mg shoot⁻¹ day⁻¹ obtained in April and June were in general higher than the rates observed in the Florida Keys by Tomasko and Lapointe (1991) during May and June, which ranged between 2 and 8 mg shoot⁻¹ day⁻¹. Dawes and Tomasko (1988) obtained values of near 7 and 18 mg shoot⁻¹ day⁻¹ for Egmont Key and near 3 mg shoot⁻¹ day⁻¹ for Anclote Key, with again no consistent pattern of growth with depth. Lapointe *et al.* (1994) and Lapointe (1992) determined rates of between 2 and 11 mg shoot⁻¹ day⁻¹ in the Keys during summer periods, and between 1 and 6 mg shoot⁻¹ day⁻¹ during the winter.

Areal Growth

Areal growth rates, which incorporate both shoot density as well as production rates, are shown in Figures 53 and 54. Areal growth was much higher at the shallow stations primarily due to higher shoot densities and demonstrated seasonal patterns, particularly at shallow sites, in response to increased above-ground growth during April and June. Peak values were typically present during shallow sites in April, but peaked at PRT-S

during June. The maximum value observed was near $5.5 \text{ gdwt m}^{-2} \text{ day}^{-1}$ for RIV-S, with remaining shallow stations exhibiting maxima near $3 \text{ g m}^{-2} \text{ day}^{-1}$.

Areal growth was high only during April at MUL and PIN, while areal growth remained high during April and June at PRT and RIV. Deep station areal growth was always less than $1 \text{ gdwt m}^{-2} \text{ day}^{-1}$. Hall *et al.* (1991) found comparable growth rates as this project observed for the shallow stations, but also determined maximum rates of near $4 \text{ g m}^{-2} \text{ day}^{-1}$ for deep control stations, much higher than any of the deep values observed during this project. Lapointe *et al.* (1994) and Lapointe (1992) determined rates between 1 and $9 \text{ g m}^{-2} \text{ day}^{-1}$ in the Keys and also discerned a clear increase in areal production (as well as shoot density and biomass) with decreasing nutrient regimes. Values determined by Dawes and Tomasko (1988) were very high at the Egmont site (8 and $12 \text{ g m}^{-2} \text{ day}^{-1}$ for deep and shallow sites respectively) but shoot density at both of these stations was substantially higher than observed at the continuous light stations.

Temporal patterns in seagrass growth in this study closely followed seasonal changes in temperature. Tomasko and Dunton (1991) suggested that low water temperatures were responsible for low blade growth rates of Halodule in January and February, despite higher light levels during this time, although the potential role of epiphytic attenuation modifying the total PAR received by the seagrass blades was not quantitatively determined. Whether observed growth is a direct response to water temperature, or additional factors, such as an increase in daily photoperiod, could not be determined during this study.

Plastochrone Interval

Plastochrone intervals (the number of days between successive blade formation) determined at all stations appear in Table 15 and turnover times in days appear in Figures 55 and 56 for all stations. Plastochrone intervals were highly seasonal and there were several samplings when no new blades were observed at a station, contrasting with periods when numerous blades were observed. From plastochrone intervals, the number of blades assumed to be produced over the preceding 60 day period was calculated and summed to determine approximate blade production per year per shoot. While the values are not statistically testable, it is interesting to note that RIV-S and RIV-D produce the most number of blades per year, while PIN-D has one of the lower annual blade reduction rates.

Turnover times are a slightly different estimate of days per unit of growth, in this case the days required (at the measured rate of growth) to completely replace shoot biomass. Periods with no new blade production will have calculated turnover times of infinity, and so data presented are median values for the station and depth. In Figures 55 and 56 and Table 15, the low growth rates (high turnover times) during December (and in February for PIN-D) are quite apparent. Turnover times for deep stations were slightly lower than for shallow stations at PRT and RIV during periods of peak growth. Minimum turnover

times (maximum growth) of approximately 30 days occurred in April and June at all stations. Growth slowed by a factor of nearly 2 at MUL-D during August and October. Work nearby in Tampa Bay (Hall *et al.*, 1991) recorded slightly higher turnover times (near 50 days) than the minima of 30 days observed for this project.

Epiphyte Biomass

Epiphyte biomass can substantially alter the light climate and dramatically affect the amount of available light to the host plant. Under conditions of heavy epiphytic colonization, growth of the host seagrass may become light-limited. The following section characterizes the epiphytic loads on *Thalassia* leaves, specifically the relationship between epiphyte biomass and above-ground seagrass biomass and the relative contribution of ash-free to total epiphyte biomass.

Ratio of Epiphyte to Above-ground Seagrass Biomass

The ratio of epiphyte biomass to above-ground biomass (blade weights) at all stations is summarized in Figures 57 and 58. Epiphyte loads were generally greatest during December and February, especially at PRT and RIV. During this period, epiphyte loads at the deep stations were as much as three times higher than *Thalassia* above-ground biomass. From April through October, epiphyte to above-ground biomass ratios were typically less than 0.5 with ratios somewhat higher at shallow sites. Decreases in the ratio were primarily the product of increasing shoot biomass in the latter months of the study as epiphytic attenuation (and loads in mgdwt cm⁻²) declined slightly with increasing blade areas.

Among shallow stations, RIV was significantly lower ($p < 0.05$) than all other stations on several occasions, while PIN-S was significantly higher ($p < 0.05$) than other stations during June. Among deep stations, most notable were the significantly ($p < 0.05$) higher ratios at MUL and PIN during February.

Project means of epiphytic loads were 1.4 mgdwt cm⁻² or 87.7 mg shoot⁻¹. While epiphytic loads are not frequently determined, the range of ratios observed in Tampa Bay during February, 0.3 to 3.0, was comparable to that observed by Kemp *et al.* (1988) and in some cases higher than that observed by Lapointe *et al.* (1994), Lapointe (1992) or Tomasko and Lapointe (1991).

Percent Ash Free Epiphyte Biomass

The contribution of ash free epiphyte biomass to total epiphyte biomass is displayed in Figures 59 and 60. From December to April, shallow stations had a higher percent of ash free epiphyte biomass than deep stations. This trend was reversed from June through October, with deep stations possessing higher ash free epiphytic loads. Overall, ash free epiphytes generally constituted only 20-40% of the total epiphyte biomass, but as noted

in the discussion of epiphytic attenuation above, contributed more heavily to attenuation. Stations that were significantly different ($p < 0.05$) from other stations were: PRT-S (December), RIV-D and PRT-D (February), RIV-S (February), and MUL-D (il).

Seagrass epiphyte loads are known to follow a seasonal pattern. Leverone (1991), Zieman and Zieman (1989), and Humm (1974) showed higher epiphyte biomass during winter and lower biomass during summer. This pattern has been attributed to the seasonal growth patterns of *Thalassia*, which, with higher growth rates during the warmer seasons, provide a relatively temporary substrate for epiphytes to accumulate. Epiphyte biomass in the current study was highest during December and February, a time when seagrass growth was minimal.

Seagrass epiphytic communities can substantially alter the light climate experienced by the host plant. Under conditions of heavy epiphytic colonization, growth of the host seagrass may become light-limited. Kemp *et al.* (1988) showed that epiphytic cover resulted in 20-40% reduction in seagrass photosynthesis in *Thalassia* growing below 1 m depth. Most of this effect was attributable to light attenuation. Epiphytes substantially reduced the amount of available light in the current study from 40-60 % in the winter and 20-50% during the summer.

During the present study, a positive relationship between total epiphyte biomass and depth was observed from December through April, when epiphyte biomass approached twice the biomass of the blades. Furthermore, it appears that calcareous or non-fleshy epiphytes were mostly responsible for this relationship. *Thalassia* productivity essentially ceased during the winter, enabling the establishment of a more permanent and complex epiphyte community. During the warmer months, when productivity was high, this relationship ceased to hold. Deep and shallow stations had reduced, but similar epiphytic biomass levels. Increased blade growth during summer could serve to maintain a cleaner blade surface area to optimize light capture (Tomasko and Dawes, 1990). However, in the present study, it does not appear to be a strategy limited to deeper grasses since they experienced leaf relative growth rates and epiphyte levels similar to shallow grassbeds. In fact, the percent of light attenuation attributed to epiphytes during the summer was approximately 20% greater at the shallow stations.

Carbohydrates

Soluble carbohydrate levels in *Thalassia* rhizome (mg gdwt^{-1}) at shallow and deep stations for each of four sites from December 1993 through October 1994 are displayed in Figures 61 and 62. Carbohydrate levels were higher in rhizomes from deep stations at all sites throughout the year. Deep station rhizomes generally contained more than 300 mg g^{-1} carbohydrate, while shallow stations rhizomes had less than 300 mg g^{-1} carbohydrate. Depth-related trends in soluble carbohydrate levels were identical to Tomasko and Dawes (1990), who conducted their studies at Mullet Key. Deep stations had higher rhizome soluble carbohydrate levels than shallow stations, which indicates that

plants at the deep edge are not sacrificing rhizome carbohydrate reserves to maintain above-ground growth.

Seasonal patterns were indistinct but a decrease in shallow station rhizome carbohydrate content was noted in June for MUL-S, PIN-S, and RIV-S. This decrease was paralleled by a decrease in shoot density, areal biomass, and leaf area index at the same stations for this month. Water clarity also abruptly declined in June, but if decreased carbohydrates represented low light stress, a reduction should be similarly evident at the deep stations as well, instead of only at shallow locations. One likely explanation is that thermal stress at the shallow stations required *Thalassia* to draw on its rhizome reserves.

Among the shallow stations, PIN usually had the lowest carbohydrate levels (significantly different at the 0.05 level in June) for all but the October sampling. PIN also showed lowest levels among the deep stations from December through April; afterward levels were similar to other deep stations.

Dawes *et al.* (1979) and Dawes and Lawrence (1980) reported that soluble carbohydrates levels in all *Thalassia* components were lowest during spring and highest in the fall, and that carbohydrates in rhizome tissues ranged from 120-360 mg g⁻¹. This seasonal pattern was not duplicated in the present study, nor were the winter and spring levels of carbohydrates as low as observed by Dawes and Lawrence. The growth conditions of the preceding year may well affect the wintertime carbohydrate levels such that if a “deficit” is present, energy storage can be replenished during periods of high productivity. Alternatively, if carbohydrate levels are above some threshold, then little investment may be made in storing nutrients, but rather used to fuel increased growth.

Sediments

Sediment parameters at shallow and deep stations for each of four sites during January 1994 are summarized in Figure 63. Deep stations had slightly finer median grain size (higher ϕ' value) than shallow stations. Among deep stations, PIN had a significantly larger ($p < 0.05$) median grain size than the other stations. Sediments were classified fine sand for all (Folk, 1974). At RIV, percent silt clay was significantly lower ($P < 0.05$) at both shallow and deep stations than their shallow and deep counterparts. Percent silt clay was higher at shallow stations than deep stations, but only at PRT was the difference significant ($p < 0.05$). Except at RIV, percent organics were also higher at shallow stations (significantly different at PRT; $p < 0.05$), while values at deep sites were generally near 0.6%.

Sediment type can affect the relative above- to below-ground biomass ratio. Burkholder *et al.* (1959) reported an increase in the ratio from 1:3 in fine mud to 1:7 in coarse sand. Tampa Bay seagrasses typically grow in muddy sand (Phillips, 1962). In the present study, no clear relationships between any sediment parameter and above- to below-

ground biomass ratios were uncovered. A greater percentage of biomass was found in blades at MUL and PIN deep stations compared to shallow stations. These deep stations, however, had less silt clay (= less muddy) than the shallow stations. Deep stations, near the edge of the seagrass meadow, were exposed to higher current velocities, and consequently, sediments would be expected to contain less silt clay and fine grains. However, as the sediment data show, these differences were not of the magnitude necessary to cause a reapportionment of biomass among the major seagrass structural components.

Photosynthetic Parameters

Parameters determined included α (initial slope of the P/E relationship), P_{max} (maximum production rates, regardless of any further increases in irradiance), E_k (“saturating” irradiance, computed as P_{max}/α), E_c (compensation point of leaf tissue, where production equals respiration), as well as chlorophyll a and b. Values appear in Table 16, and indicate that of the few station-to-station differences apparent, no consistent variations with depth were present, and the largest changes noted were in the differences between the April and June samplings. Between the two samplings, chlorophyll concentrations increased by a factor of 2 to 4, E_c values were substantially reduced, E_k was lower, P_{max} was higher by a factor of near three, and the photosynthetic efficiency, α , increased by factors ranging from 1.4 to more than 14.

The overall results are consistent with an increase in photosynthetic efficiency necessitated by the reduction in both water column and blade-available (after epiphytic attenuation) PAR. Seasonal decreases in water clarity were observed at all station during this period.

Not all stations, however, appear to utilize stored energy reserves to adjust to the lowered light conditions (Figures 61 and 62). Only two of the four deep stations (MUL and PRT), exhibited reduced carbohydrate levels between April and June. Three of the four shallow stations (all except PRT) had reduced rhizome carbohydrate values, but this has been linked to thermal rather than low light stress, as PAR was not expected to be limiting at shallow stations. Implied is that the compensation for lowered light can be rapidly effected and at a relatively low cost in energy to the plant, or at least at a cost that can be overcome in a 60 day period.

The increases in chlorophyll as a result of lowered light levels is consistent with patterns observed both elsewhere, and for other species (Wiginton and McMillan, 1979; Dennison and Alberte, 1985; Dawes and Tomasko, 1988; Goldsborough and Kemp, 1988). Although differences in chlorophyll content were noted between seasons, however, there were little consistent difference between depths, despite obviously different PAR levels. The lack of difference between shallow and deep station chlorophyll content is consistent with the results observed by Dawes and Tomasko (1988).

The P_{max} parameter was unusual in that it increased between April and June, over a period when light was reduced. The increase in P_{max} was contrary to patterns observed by others, in which the parameter is reported to decrease with decreasing light (Dawes and Tomasko, 1988; Tomasko, 1993b). Dunton and Tomasko (1994), however, did record higher P_{max} in conjunction with higher chlorophyll and lowered PAR levels. The monthly mean P_{max} values for this work ($47.5 \mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1}$ for April and $143.8 \mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1}$ for June) approximate the measurements of Dawes and Tomasko (1988) who recorded peak production rates of between 43.3 and $105.1 \mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1}$. In contrast, the P_{max} values for the project were substantially less than the measurements of Fourqurean and Zieman (1991a) which ranged from 171 - $256 \mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1}$. Comparisons of deep and shallow stations indicated that where significant differences existed, shallow stations recorded higher P_{max} values, in contrast to the seasonal response to lowered light.

Values obtained by Dawes for compensation irradiance in this study ranged between 10 and $90 \mu\text{E m}^{-2} \text{ sec}^{-1}$ with an overall average from all stations in April and June of $42 \mu\text{E m}^{-2} \text{ sec}^{-1}$. Other published values appear in Dawes and Tomasko (1988), in which E_c ranged between 24 and $45 \mu\text{E m}^{-2} \text{ sec}^{-1}$. Fourqurean and Zieman (1991a) determined the compensation irradiance values for leaves of *Thalassia* to be near $15 \mu\text{E m}^{-2} \text{ sec}^{-1}$. Methodological differences between the two researchers (blade sections versus entire shoots) may account for some differences, but other factors being equal, one would expect higher rather than lower E_c values from the use of an entire shoot due to the respiratory demand of the shoot portion. Differences may have arisen from the equilibration procedure of Fourqurean and Zieman (1991a) in which *Thalassia* from Florida Bay received daily 12 hour periods of $500 \mu\text{E m}^{-2} \text{ sec}^{-1}$, totaling $21 \text{ E m}^{-2} \text{ day}^{-1}$, compared to the 5 - $10 \text{ E m}^{-2} \text{ day}^{-1}$ to which Tampa Bay *Thalassia* was exposed. Other pertinent differences may include measurements of irradiance or method of curve fitting to solve for the photosynthetic parameters.

Photosynthetic efficiency, α , for the project, ranged between 0.22 and $1.31 \mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1} (\mu\text{E m}^{-2} \text{ sec}^{-1})^{-1}$, with higher efficiencies reported for June. The results again suggest a seasonal acclimation to decreased irradiance, but examination of α with depth indicate a significant ($p < 0.05$) increases in photosynthetic efficiency at shallow, non-light-limited stations. Values observed were somewhat lower than the α determined for Anclote and Egmont Keys Dawes and Tomasko, 1988) where values between 1.05 and $1.72 \mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1} (\mu\text{E m}^{-2} \text{ sec}^{-1})^{-1}$. Fourqurean and Zieman (1991a) obtained values between 0.42 and $0.58 \mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1} (\mu\text{E m}^{-2} \text{ sec}^{-1})^{-1}$. The lower efficiency observed by Fourqurean and Zieman (1991a) again may be attributed the high light levels under which their plant material was equilibrated and the acclimation of Tampa Bay material to lower light levels.

Saturating irradiance (E_k) ranged between 180 - $282 \mu\text{E m}^{-2} \text{ sec}^{-1}$ in April, decreasing to between 75 and $200 \mu\text{E m}^{-2} \text{ sec}^{-1}$ in June. Decreases in E_k with decreased PAR are consistent with increased P_{max} and increased photosynthetic efficiency. E_k values

determined for the project were approximately half that determined by Fourqurean and Zieman (1991a), and can again be explained by conditions of acclimation or perhaps calculation techniques.

Seasonal variations in photosynthetic parameters exceeded station variability, and consistent, depth dependent patterns in photosynthetic parameters were generally absent for *Thalassia* at the Tampa Bay sites. While seasonal variations in photosynthetic parameters were coincident with a reduction in average water column clarity (attenuation coefficients, or average monthly PAR) between April and June, the reduction in total irradiance was not as visible in depictions of average daily total PAR recorded during the growth periods. The effective light history of the plant material may extend beyond the two week period which was evaluated for H_{sat} . It is also evident that greater variation in light climates exists between shallow and deep stations than between the two growth periods. Comparable or greater variations in light climate experienced between shallow and deep stations (see below) were not observed within a monthly data set. Probable thermal stress at all shallow stations except RIV may alter adaptive strategies, requiring that additional production be supported to offset the increased respiration demands.

Light Climate

Results of light conditions at each station during the determinations of growth rates are presented in subsequent sections. Calculated for the roughly 14 day time periods between marking and recollection of *Thalassia* shoots, parameters include average daily bottom irradiance, the number of hours per day that bottom irradiance was greater than calculated saturation values (H_{sat}), and the number of hours per day that bottom irradiance was greater than calculated compensation values of leaf tissue alone ($H_{comp-leaf}$).

Water column PAR measurements were adjusted for the mean epiphytic attenuation determined on shoots from each station and depth such the adjusted PAR values represent the PAR actually received by the *Thalassia* blades. Data for shallow stations were extrapolated using deep station water column attenuation coefficients and shallow stations epiphytic attenuation values. Individual sensor failures produced missing data during December, February, and April for some locations.

The E_{c-leaf} Parameter, the irradiance sufficient for production to balance respiration of leaf tissue, is a known underestimate of the irradiance required to maintain an entire plant with a net positive carbon balance. Fourqurean and Zieman (1991) state that $E_{c-plant}$ can be twice as great as E_{c-leaf} and differences in reported values of E_c are often due to the inclusion of the respiratory demands of varying proportions of non-photosynthetic material in the calculation. The effect of variation in leaf percent biomass, for example, can be substantial, ranging from an E_c of $25 \mu\text{E m}^{-2} \text{ sec}^{-1}$ at 30% leaf biomass to $85 \mu\text{E m}^{-2} \text{ sec}^{-1}$ at 8% leaf biomass. Relative apportionment is highly variable within a given site (Fourqurean and Zieman, 1991a; this project) and may be controlled by factors associated with sediment grain size, nutrient supply and stability (Zieman, 1982).

Additionally, tissue percentages may reflect the physiological condition of the seagrass bed and response to stress (Dunton, 1994).

Saturating and compensation irradiance values were provided for the April and June samplings by Dr. Clinton Dawes and were specific to both site and depth of station. These data were used directly to calculate H_{sat} and $H_{comp-leaf}$ for the May and June data sets and therefore have the highest confidence. Data were unavailable for the remaining samplings, and although photosynthesis/irradiance parameters have been observed to vary both seasonally and with depth (Kemp *et al.*, 1988; Tomasko, 1993b; Dunton and Tomasko, 1994), the overall mean of E_k and E_{c-leaf} as determined in April and June, was used to calculate very rough approximations of H_{sat} and $H_{comp-leaf}$ for the remaining samplings for the purposes of inter-station comparisons.

Additionally, E_{c-leaf} does not account for the varying respiratory demands exacted by the non-photosynthetic tissues, and the $H_{comp-leaf}$ presented below is a substantial overestimate of the H_{comp} required for the whole plant. Annual carbon budgets were not computed due to the lack of a coherent, seasonally specific data set including P/E parameters as well as determinations of respiration at the relevant temperatures of all samplings.

Average Daily Total PAR

Average daily total PAR (daily quantum flux, $E\ m^{-2}\ day^{-1}$) at shallow and deep stations for all sites is shown in Figures 64 and 65. Shallow stations sustained higher light levels than deep stations, despite the generally higher epiphytic loads at shallow stations. Light levels at shallow stations were also extremely varied, with most inter-station comparisons significantly different. Except for PIN, deep stations experienced similar light levels throughout the year, ranging roughly between 5 and 13 $E\ m^{-2}\ day^{-1}$.

Maximum values of average daily PAR were typically observed in April and June and generally coincided with periods of maximum shoot and leaf relative growth rates. In the case of PIN-S and PIN-D, however, growth occurred even though there was no corresponding increase in available PAR, and observed growth was comparable to MUL-S and MUL-D, where PAR levels received were much greater. Values at RIV-D were extremely low during August, presumably due to the high color (and associated lower salinities) observed in the water column during this sampling.

A seasonal signature in daily PAR totals is evident at most sites, particularly MUL-S and PRT-S, and probably for RIV-S. Average daily PAR was relatively unchanged throughout the year at PIN-D, with the deep station receiving less than $10\ E\ m^{-2}\ day^{-1}$ during all six sampling periods. PIN consistently had lower light levels (at both shallow and deep stations) than all other sites. Maximum PAR day-1 approached $30\ E\ m^{-2}\ day^{-1}$ at the RIV-S site in June, but no comparable increases of any growth parameters was noted for this station and time period. In fact, shoot density declined at RIV-S during June, as did above-ground biomass and rhizome carbohydrate, indicating a response to

thermal stress. Photoinhibition to the extent where net production was negative, however, did not occur at this site.

H_{sat} (Adjusted for Epiphytic Attenuation)

The average number of hours above saturating ix-radiance for leaf tissue is shown in Figures 66 and 67. Highest exposure to saturating irradiance at both shallow and deep stations occurred during the April and June samplings with station to station and depth variations mimicking the patterns observed in total daily PAR. June H_{sat} values were generally the largest observed, although the fact that high growth rates are observed in April argue that H_{sat} and growth are either temporally decoupled, or that the relationship between light and growth plateaus, with increasing time at or above H_{sat} resulting in no additional growth.

Shallow stations typically experienced between 6 and 11 hours of saturation irradiance daily during each of the samplings. Saturating irradiance of hours per day or more was consistently attained at MUL and PRT deep stations, and, except during August, also at RIV. Maximum values of H_{sat} at deep stations ranged between 6 and 9 hours. During August, RIV averaged only 1.5 hours day⁻¹ of saturating irradiance, most likely due to the onset of the wet season and high color values noted by samplers and the subsequent increase in water column attenuation. The PIN deep station, however, on average received less than 3 hours day⁻¹ of saturating irradiance throughout the year and the PIN shallow site did not exceed 9 hours day⁻¹ day even during June when maximum values were obtained.

Dennison and Alberte (1985) determined that light-limited *Zostera* growing near the deep edge during the summer appear to be living near the minimum light regime for growth and survival ($H_{sat} = 6$ to 8 hours). Deep *Thalassia* in this study received generally between 6 and 9 hours saturating irradiance during April and June, with biomass changes attributable to shading response evident at PIN deep where H_{sat} was only 3 to 6 hours. Values of H_{sat} at months other than April and June should not be used to compare between samplings as they are generated from E_k values determined in April and June. With this caveat, however, PIN-D continues to exhibit lower periods of time above E_k than the remaining deep stations.

($H_{comp-leaf}$ Adjusted for Epiphytic Attenuation)

Average number hours above compensation irradiance for leaf tissue is shown in Figures 68 and 69. All stations received at least six hours of compensation irradiance throughout the year, except RIV during August, when freshwater influences and associated color was high. Stations are remarkably similar, in fact, with all shallow stations ranging between 8 and 14 hours day⁻¹ over the year. Shallow stations typically received 0-2 hours more compensation irradiance than their deep station counterpart.

The longest daily light period above compensation irradiance for both shallow and deep stations occurred in June. The PIN site (both shallow and deep) had significantly lower ($p < 0.05$) time at or above $H_{comp-leaf}$ than other stations during April.

Interrelationships of Growth and Abiotic Factors

The design of the study provided paired data such that epiphytic attenuation, carbohydrates, growth determinations, and biomass measurements were all performed on tissues from a single shoot. H_{sat} and $H_{comp-leaf}$ were calculated for samplings for which photosynthetic data were available, and the values were determined both for water column conditions and after attenuation by shoot specific epiphytes. Data were segregated by deep and shallow stations and interactive multiple linear regression performed on the various growth parameters as a function of carbohydrate content, and average PAR values, total daily PAR, H_{sat} , and H_{comp} . No significant relationships were determined between growth parameters and calculated light parameters. In general, above-ground biomass was a better predictor of the various growth measurements than were the light levels received.

The relationship between underwater light and blade growth is complex and seasonal rhythms of growth are strong, even for highly stressed communities (Hall *et al.*, 1991) with minimal resources on which to draw. Tomasko and Dunton (1991) found no relationship between blade growth of *Halodule* and the percent of days when irradiance exceeded $1,000 \mu\text{E m}^{-2} \text{ sec}^{-1}$. Low water temperatures appeared responsible for low blade growth rates in the winter, despite higher light levels.

Thermal cues may also control growth rather than PAR levels (Dunton and Tomasko, 1994), and in this study, periods of higher PAR are not necessarily matched by increases in growth. Shading responses can include an increased above-to below-ground ratio or increased blade length (Dunton, 1994) which may actually have an inverse relationship of production with light. In this study, for example, the PIN-D station exhibits numerous examples of potential low light stress responses, and yet blade growth rates, station biomass, and below-ground resources (as carbohydrate content) remain high. Species with substantial storage of carbohydrates can effectively decouple photosynthesis and expressed growth. As a result, modeling *Thalassia* short term response to light levels or to inadequate light levels remains an uncertain process.

SUMMARY

The investigation of *Thalassia* light requirements used continuous scalar light measurements at two depths in the water column and periodic seagrass community assessments to define the light climate (and the seagrass response) at the deepest edges of the *Thalassia* beds. The amounts of photosynthetically active radiation (PAR) attenuated by the water column and by the epiphytic community on the seagrass blades were each quantified to determine the PAR actually available to the *Thalassia* blades. Annual or seasonal values of light obtained were to be considered as the light “requirement” of the species. The conclusions would be tempered, of course, by the responses or conditions of the beds as measured over the course of the project, and by whether water clarity during the project year was representative of typical conditions. Light requirements so determined were to be compared to water clarity data available for other portions of Tampa Bay to determine the likelihood of reaching established seagrass restoration targets.

Care was taken to select sites which appeared to be light-limited at the maximum depths, and which were in areas where seagrass areal coverage was stable (*i.e.*, presumably stable water quality conditions). Four stations in Lower Tampa Bay were established and each instrumented with continuously recording equipment. Stations were located at Mullet Key (MUL), Point Pinellas (PIN), Port Manatee (PRT), and in the mouth of the Manatee River (RIV). Elevations of the deep edges ranged between 1.63 m (at RIV) and 2.04 m (at PIN) relative to mean lower low water (MLLW). There were no depth limited *Halodule* beds nearby. Temperatures and average salinities at all deep stations were within published ranges for *Thalassia* and were very comparable, although RIV (and to a lesser extent PRT) experienced periods of abruptly lowered salinity with the onset of the wet season in late summer.

Instruments consisted of two scalar (4π) PAR sensors, separated by a vertical distance of 0.5 m, thus permitting the calculation of attenuation coefficients, the exponential rate of decline of PAR with depth in the water column. Errors due to bottom reflectance were demonstrated to be minimal. Water column clarity at shallow stations was usually comparable to clarity at the deep stations, but at PIN, a significant bias indicated that micro- or meso-scale circulation patterns or wave action and sediment resuspension could produce significantly different water column clarity within very short distances. Within 100-200 m distances, differences of PAR at equivalent depths could vary by as much as 5% (20% versus 25%). The observed difference decreases the confidence of extrapolating deeper water column measurements to nearshore environments.

At each site, bimonthly growth and quarterly biomass measurements were performed on *Thalassia* both at the maximum depth limits and at a shallower (and therefore non-light-limited) station to evaluate the types of changes which could be expected along light gradients. As the shallow stations were not light-limited, water column attenuation

measurements were used to extrapolate absolute levels of PAR from the deep to the shallow stations, for aid in interpreting the results of the biological condition analyses, despite the potential errors.

Expected seasonal patterns of *Thalassia* biomass were evident in all of the biomass parameters. April and June typically contained the maximum values, while December and February exhibited the minima. Seasonal changes often exceeded inter-station differences and were more pronounced at the shallow stations. Gradients of decreasing above ground biomass, shoot density, and leaf area index with increasing depth were quite apparent. At stations other than PIN, mean blade length per shoot was longer at shallow stations, but differences were often not significant. Shoot density and biomass values were lower than other researchers had obtained at study sites nearby (Hall *et al.*, 1991; Dawes and Tomasko, 1988). Salinity stress at RIV following a rapid onset of the wet season and discharge from the Manatee River resulted in exfoliation and a decrease in biomass, leaf area per shoot, and leaf area index.

Evidence of thermal stress was observed in June at all shallow stations with the exception of PRT. A decline in shoot density during June was particularly evident at MUL-S. The June sampling also recorded a decline in rhizome carbohydrate content at shallow stations, again except for PRT. PIN-S in particular is marked by a drop in carbohydrate content to less than 150 mg gdwt⁻¹. Carbohydrate declines appeared linked to thermal stress, rather than coincident decrease in water clarity as similar declines in carbohydrates were not observed in deep station tissues. Deep stations had larger concentration of carbohydrates in the rhizomes than did shallow stations and seasonal patterns at deep stations were not apparent.

Thalassia tissues were apportioned to blades, shoots, and combined roots and rhizomes as 23%, 37%, and 40%, respectively, for the project as a whole, but seasonal patterns of growth produced a range of 20-35% in blade tissues with a large amount of variation within a given sampling and station. Overall, PIN-D stands alone in having a higher percentage of its biomass allocated to blade material during all samplings. Most notable during May, the high blade percentage is a combination of both longer blade lengths and lower weights of rhizomes. Increased blade lengths persisted at PIN-D from April through the October sampling but were particularly evident in August. Increased blade lengths are one of the typical morphological responses produced by shading (Hall *et al.*, 1991; Goldsborough and Kemp, 1990).

Ratios of above to below ground (A:B) biomass at PIN-R were consistently high in comparison to other stations and consistent trends with depth were not observed. Dunton (1994) reports an increase in A:B ratio under low light stress for *Halodule* and the conditions at PIN-D may indicate a response to lowered PAR values. Potential light stress at this site is consistent with the lower annual PAR received at depth (in comparison to other stations) and the observed decrease in shoot density between initial and final project samplings.

Growth parameters (leaf relative growth rate, above ground growth per shoot) demonstrated no depth-related patterns, but exhibited seasonal maxima during April and June. Areal growth peaked in April, integrating typically higher shoot densities and shoot relative growth rates observed during this month. The longer mean blade lengths at PIN-D were reflected in the higher growth per shoot noted for this station in June, August, and October. PIN-D was again noteworthy in the low numbers of blades per year produced in comparison to other deep stations. The number of blades per year produced was based on both calculated plastochrone intervals during this project, and the average inter-cohort distance of the last several years, as determined by reconstructive aging analyses.

PIN consistently had lower light levels (at both shallow and deep stations) than all other sites. The highest PAR per day observed approached $30 \text{ E m}^{-2} \text{ day}^{-1}$ at the RIV-S site in June, but no comparable increases of any growth parameters were noted for this station and time period. In fact, shoot density declined at RIV-S during June, as did above-ground biomass and rhizome carbohydrate, and was attributed to thermal stress. There was no temporally immediate relationship between H_{sat} (or other light parameters) and growth, even though PAR available to the plant was quantified at a shoot level by accounting for epiphytic attenuation. Deep *Thalassia* in this study was estimated to receive PAR equal to between 6 and 9 hours of leaf saturating irradiance during April and June. At PIN-D where biomass changes attributable to shading response were evident, H_{sat} was only 3 to 6 hours.

The overall picture from the condition and growth measurements is that PIN-D began to exhibit evidence of morphological adaptations to decreases in PAR during this study. Adaptations primarily consisted of increased blade lengths and decreased numbers' of blades produced, which in turn affected a number of parameters. Ratios of blade area to tissue weights indicate that the increased blade area at PIN-D had less structural support. Lower below ground tissue proportions at PIN-D than at other stations may also reflect cumulative low light stress, but the carbohydrate content of the remaining rhizome tissues was not significantly affected. On the other hand, the thermal and salinity stress which occurred at three of the shallow Tampa Bay sites were short term events which exerted an immediate reallocation of resources for *Thalassia*, *i.e.*, decline in storage of rhizome carbohydrates, but from which the plant apparently recovered quickly.

Other evidence, as well, indicates that the PIN-D station was under stress. In the analysis of *Thalassia* bed stability at the maximum depth limits over the course of the project, shoot density at PIN-D suffered a significant net decline between the December and the October sampling, despite the fact that seasonal patterns in shoot density would predict that October densities would be higher than the December values. Other stations in the study either displayed the expected increase in shoot density or were unchanged. Blade production per year was lower at PIN-D than other deep stations, and the leaf scars enumerated indicated that the low blade production had been going on for some

years. The lower below ground biomass (and higher A:B ratios) seen at PIN-D during all samplings also argues that plant resources have been diverted from typical allocation patterns for some time, as differences between sediments at the deep stations are not sufficient to explain the higher ratios. It is unknown at this time whether the stress experienced by PIN-D can be tolerated indefinitely or will result in increasing declines in the shoot density of the deep edge.

With the knowledge that PAR at one of the deep stations may be at unacceptable levels, or at the least that morphological adaptations to shading were triggered, the light climate may be examined knowing that the data encompasses a threshold value. Based on other monitoring programs within the Bay, annual average water clarity in 1994 in most segments was comparable to the recent data (1985-1990), although some seasonal patterns in clarity were different. (Water clarity in Hillsborough, however, is apparently still improving). With Lower Tampa Bay water clarity during the project year comparable to previous conditions, grassbeds can be presumed to be at a steady state with respect to light. As a result, the PAR received at the maximum depth limits during the project may be more confidently expected to represent true ecological compensation points, or the PAR necessary to support a stable grassbed, balancing growth with normal mortality, grazing, and repetitive minor stresses.

Maximum depth limits of the *Thalassia* beds sampled in the project ranged between 1.63 and 2.04 m (MLLW) in the Lower Tampa Bay, with elevations (referenced to MLLW datum) some 0.34 m below mean tide levels. Station depths were determined from predicted tides, depth observations while on station, and had a typical standard error of 0.02 m, with a resulting precision in PAR percentages of near $\pm 2\%$. Water column depths used for calculation of PAR attenuation were 2.10 m, 2.37 m, 2.15 m, and 1.98 m for MUL, PIN, PRT and RIV, respectively.

Annual averages of water column attenuation coefficients ranged between 0.80 to 0.94 m^{-1} with median values between 0.73 m^{-1} and 0.88 m^{-1} . Relationships of maximum depth with attenuation coefficient were consistent in that the station with the deepest maximum depth (PIN) recorded the lowest attenuation coefficients (clearest water). Water clarity during the growing season (May-September) was substantially less with average attenuation coefficient ranging between 0.89 and 1.17 m^{-1} during this period as typical annual cycles of increased chlorophyll and color were manifested.

Annual and seasonal light percentages were calculated from the continuous record of attenuation after each reading had been converted to a percentage of subsurface scalar ix-radiance (rather than from annual or seasonal averages of K), to avoid underestimating percentages of PAR received at depth. Data used were taken only from periods between 1000-1400 hours to facilitate comparisons with other monitoring programs which typically endeavor to collect attenuation data during a midday time period.

Annual percentages of PAR present in the water column at the maximum depth limits of *Thalassia* averaged 22.5% of subsurface scalar irradiance. **Percentages represent attenuation by materials in the water column only and can be transferred to other areas as appropriate management targets only if epiphytic growth is comparable.** PAR percentages present during the growing season were somewhat less, ranging between 14.5% and 18.0%.

The epiphytic growth on *Thalassia* blades can be substantial and during this study resulted in an additional 7-67% reduction in light actually available to the seagrass blades, with an average annual reduction of between 32% and 34% at the four stations. Evidence from more restricted lagoonal environment (Sarasota Bay) indicate annual average epiphytic attenuation can be nearer 50% (Dixon and Kirkpatrick, 1995), and epiphytic growth in the higher nutrient regimes of Hillsborough Bay (HCEPC, 1990; Zarbock *et al.*, 1994; Janicki and Wade, 1994) is expected to be even greater based on the numerous reported responses of epiphytes to increased nutrient regimes. Seasonal patterns of epiphytic loads are higher in the winter and appear linked primarily to patterns of *Thalassia* blade growth and the length of time blade material remains available for colonization.

To look at *Thalassia* PAR requirements with independently varying attenuations due both to water column materials and epiphytes, water column percentages of PAR were further reduced by the station-specific epiphyte attenuation measured during the bimonthly samplings in order to compute **total attenuation**. Annual averages of PAR actually available to the *Thalassia* blades (adjusted for both water column and epiphytic attenuation) were between 13.9% and 14.2% of scalar subsurface irradiance for MUL, PIN, and RIV, while at PIN where low light stress appears likely, 13% was received. **The percentages of total attenuation (13-14%) are not appropriate water column management targets, unless epiphytes on *Thalassia* are completely absent.**

The scatter in annual average PAR between the stations is much less when the attenuation due to both water column and epiphytes is considered and the relationship of maximum depth limits with **total** attenuation (Figure 27) is improved over relationships with water column attenuation alone. The improvement (and the strength of the relationship) lends support to having defined a functional and accurate value for light requirements for *Thalassia* of near 14% of subsurface scalar irradiance. What is remarkable is that the PIN station, showing evidence of low light morphological adaptations, received only about 1% less or 13% as an annual average. In addition, monthly PAR percentages (Table 8) reveal that PIN received lower levels of PAR than the other stations between January and May, while MUL, PRT, or RIV received lower PAR levels than PIN during most of the months of the growing season.

PAR “deficits” incurred during winter, early spring, and into May are apparently sufficient to trigger morphological responses which extend through the fall. Since growth is effectively decoupled in time from PAR received, an important conclusion is that

monitoring during the growing season alone to assess water clarity target compliance is not appropriate.

When PAR beyond the 1000-1400 hour window is included in the consideration, differences at PIN and the resulting morphological changes become more distinct. Annual totals of PAR in the water column at MUL, PRT, and RIV ranged between 4,860 and 4,930 E m⁻² year⁻¹ (Table 9), while PIN received only 3,640 E m⁻² year⁻¹, 75% of that received by stations which displayed no shading responses. During daylight hours, PAR at the PIN maximum depth averaged 10.0 E m⁻² day⁻¹ compared to 13.3-13.4 E m⁻² day⁻¹ at the other three stations. When water column PAR is adjusted for epiphytic attenuation, annual totals of PAR received by the *Thalassia* blades ranged between 3,060 and 3,140 E m⁻² year⁻¹ for MUL, PRT and RIV, while PIN was again near 75% of these levels, or at 2,240 E m⁻² year⁻¹.

In comparison to *Thalassia*, the best available *in situ* estimates of light requirements for *Halodule* (Dunton, 1994) are described as a range of 2100-2400 E m⁻² year⁻¹ to maintain consistent levels of biomass under low epiphytic conditions. Biomass declines and eventual *Halodule* loss were noted when annual water column PAR totals was measured at 2200 E m⁻² year⁻¹ with noticeable epiphytic coverages. Epiphytic attenuation was not quantified directly, however.

Mapping of seagrass coverages in 1950 and 1990, coupled with distribution of coverage by depth classifications (percentage of seagrass coverage in 0-0.5 m, 0.5-1.0 m, etc.), was used to define seagrass restoration and depth targets (Janicki *et al.*, 1994) from a 1950 benchmark period. Seagrass restoration targets were phrased in terms of allowing the return of seagrasses to 1950's acreages, and, for modeling purposes, segment-specific target depths were identified; 1.0 m for Hillsborough Bay, 1.5 m for Old Tampa and Middle Tampa Bays, 2.0 m for Lower Tampa Bay (Janicki *et al.*, 1994). Target depths are relative to chart datum, or mean lower low water, and were conservatively selected to encompass approximately 95% of the maximum depth limits of seagrasses observed for each segment during 1950 (Coastal Environmental, 1995).

Interestingly, only one of the four stations instrumented during the project had seagrasses at or greater than the target depth of 2.0 m MLLW for Lower Tampa Bay. At PIN, where the maximum depth limit was 2.04 m MLLW, annual PAR was also much lower than for other stations and the *Thalassia* community at this station exhibited morphological adaptations to shading. Remaining stations ranged between 1.63 and 1.81 m MLLW. As water clarity in Lower Tampa Bay has been relatively stable over the last number of years, seagrass maximum depths at three of the four stations are not expected to increase substantially, and maintaining present water clarity is not expected to result in expansion to 2.0 m MLLW depths at these locations. It is unknown whether the target depth can be maintained at the one station evidencing shade adaptations.

The areal extent (and, presumably, depths, as well) of seagrasses at the four stations monitored, however, may already be comparable to the target 1950's areal distributions. The stations were located in areas with relatively small historical losses at the deep edges of the seagrass beds. The combined vertical and horizontal resolutions of the mapping does not permit a determination as to whether the present maximum depth limits at the stations sampled are equivalent to the 1950 depth limits at the same locations.

With knowledge of the light requirements and average attenuation coefficients, target depths can be rephrased as to whether a particular percentage of PAR is present at a specified depth. If seagrasses are not present, although water clarity requirements appear to be met, contributing causes could include potential lag times in recolonization, lack of adequate seed stocks, epiphytic growth higher than estimated (with subsequent reduction of PAR), intermittent sampling not adequately capturing extreme attenuation events, nearshore light climates significantly lower due to wave action or other terrestrially-based influences, or overall depth on station.

Light requirements determined during the project were used together with other monitoring program results (COT, HCEPC) to evaluate the suitability of the light climate during 1994 in other portions of Tampa Bay for *Thalassia*. The extrapolation of light requirements determined in Lower Tampa Bay to other segments is based on the assumptions that 1) epiphytic loads are either comparable or can be accurately estimated for the regions of the Bay with higher nutrient loads, 2) that transformation of Secchi depths to PAR attenuation are sufficiently accurate, 3) that an intermittent sampling program adequately reflects annual totals, and 4) that nearshore light environments are comparable to stations in the vicinity but in deep waters offshore.

Extrapolation to other regions of the Bay, given the qualifiers described above, indicated that the areas of the Bay where the nearest stations met water clarity requirements were generally near those regions which have exhibited little loss of grasses at the deeper edges, while stations near areas of large losses generally do not meet light requirements at target depths. (Exceptions were in the region at the head of Hillsborough Bay, where water clarity may be suitable, but salinity regimes undoubtedly restrict the species which can survive in this region.) Evaluations were performed using both the epiphytic attenuation measured for Lower Tampa Bay (approximately 30% attenuation), and using the higher epiphytic attenuations (near 50%) determined in Sarasota Bay to the south. (Even the higher Sarasota Bay value may not adequately reflect the epiphytic growth possible in the high nutrient regimes of Hillsborough Bay, or the interaction of high light and high nutrients as experienced by shallow stations.)

The coincident pattern of regions which fail to meet targets and which have also lost large areas of seagrass is additional indirect evidence that lowered light levels were responsible for the losses in coverage at the maximum depths and that light requirements are approximately correct. Water clarity has not noticeably improved in most segments of the Bay (with the exception of Hillsborough Bay) since 1990. Unless the deep edges

of seagrass beds in 1994 has increased substantially since 1990, failure to meet water clarity targets, rather than lag times for recolonization, appears to be the controlling factor for coverage at maximum depth limits.

It will be instructive to repeat the change analysis of seagrass coverage, as is being performed by the SWIM Department of SWFWMD at the present time (1995), as the restoration targets were developed with seagrass coverage determined in 1990. Hillsborough Bay water quality appears to have continuously improved since the 1970's and increases in seagrass coverage in this segment should reflect improving water clarity, tempered by the lag times necessary for the various species to recolonize the segment.

In summary, annual **water column** minimum light requirements are near 22.5% for *Thalassia* at the level of epiphytic cover observed during the study. Epiphytic cover is expected to increase with increasing nutrients, or distance up the Bay. To accurately extend the light requirements determined in the present study to other areas, site specific epiphytic attenuation data should be obtained. A conservative estimate of epiphytic attenuation (50 %), with a resulting water column requirement of 27.6% has been used for the upper portions of the Bay, but the actual values of epiphytic attenuation and therefore water column requirements are unknown. Based on data from other studies, light requirements for *Halodule* appear to be roughly equivalent or potentially higher than for *Thalassia*.

The maximum depth limits of three of the four stations instrumented in Lower Tampa Bay do not currently meet the seagrass restoration target depths and water clarity recorded at the four locations would not permit the extension of the *Thalassia* beds to the target depths. The station which does meet the depth target exhibited morphological changes in response to shading, and the long term success of the *Thalassia* bed at the 2.04 m (MLLW) depth of the station is unknown. The results are consistent with the five year averages of monthly Secchi depths (1985-1990) from Lower Tampa Bay which indicate that 22.5% of subsurface scalar irradiance is present at 2.04 m of water column depth (Janicki and Wade, 1994), or 1.70 m MLLW after conversion from mean tide level. Maintaining present water clarity is not expected to result in further depth extensions, at least for the four sites studied in Lower Tampa Bay.

Even if unadjusted for the probable increases in epiphyte load with higher nutrient loads, stations in areas with stable water quality, and near areas where large historical losses of grasses have occurred, do not generally meet water clarity requirements at target depths. Implicit is that maintaining present nutrient loading and water column clarity conditions will not result in increases in the maximum depths of seagrass cover.

The probable lack of depth extensions under present water clarity conditions is a phenomenon that is separate from the losses and recoveries of seagrasses at shallow and non-light-limited areas. Losses at both shallow and deep sites indicate that processes beyond simple water column light attenuation are at work. Losses in the shallows rather

than at depth could be attributable to many causes, but are consistent with a number of factors, including higher epiphyte loads under high light and increased nutrient levels as described by Tomasko and Lapointe (1991), episodic exposure, thermal stress or desiccation under extreme low tides, or overgrowth with macroalgae.

The general co-location of historical losses and failure to meet water clarity targets pertains to Hillsborough Bay as well. The continuing improvement in water quality in this Bay segment, however, and a lack of knowledge of lag times between improved water quality and return of a particular seagrass, makes any predictions of the eventual outcome in Hillsborough Bay under current nutrient loadings very uncertain. Updated mapping (presently underway) and comparison with 1950 benchmark coverages will provide material for additional inferences.

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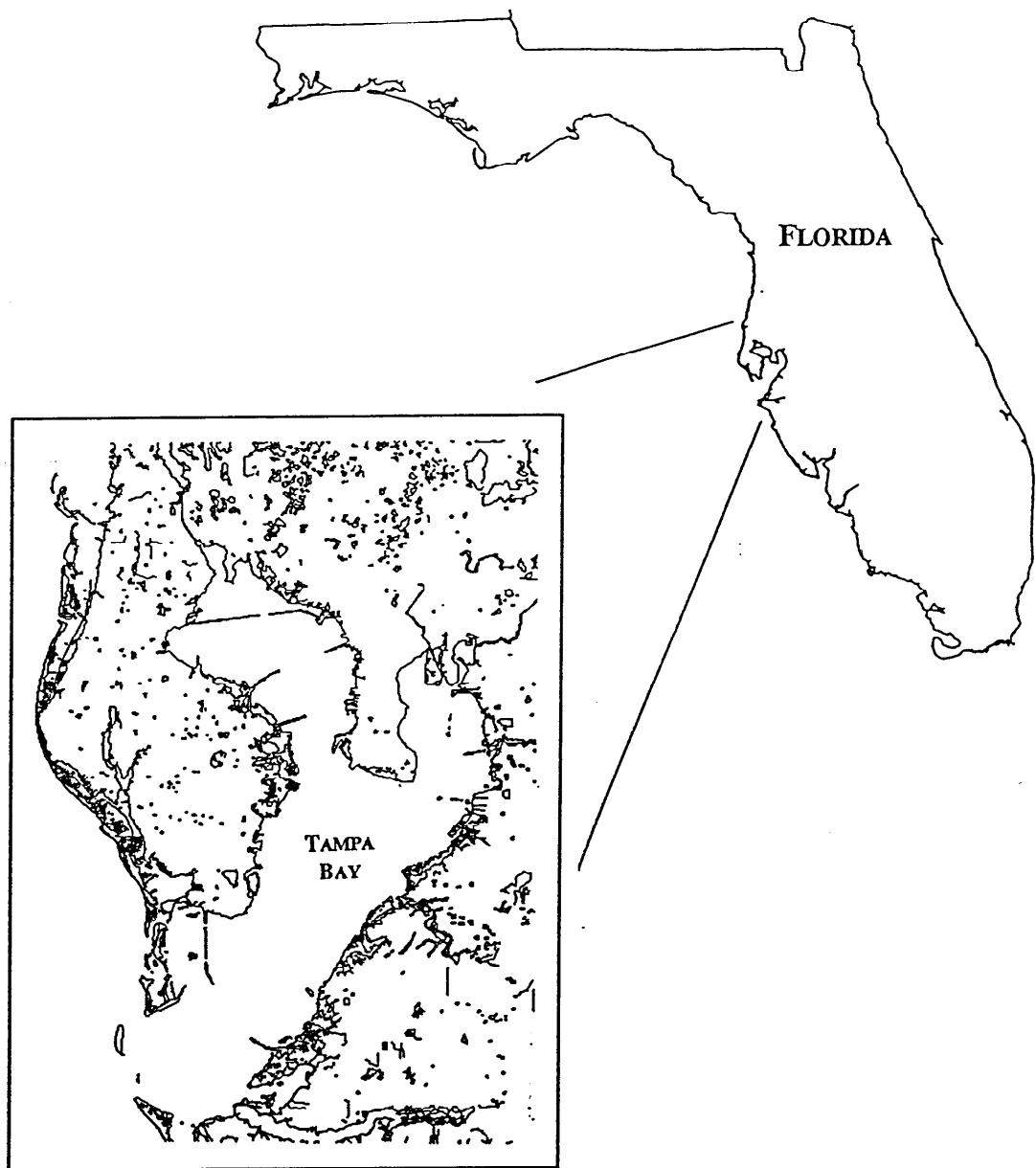


Figure 1. Study location for the determination of light requirements of *Thalassia testudinum* in Tampa Bay.

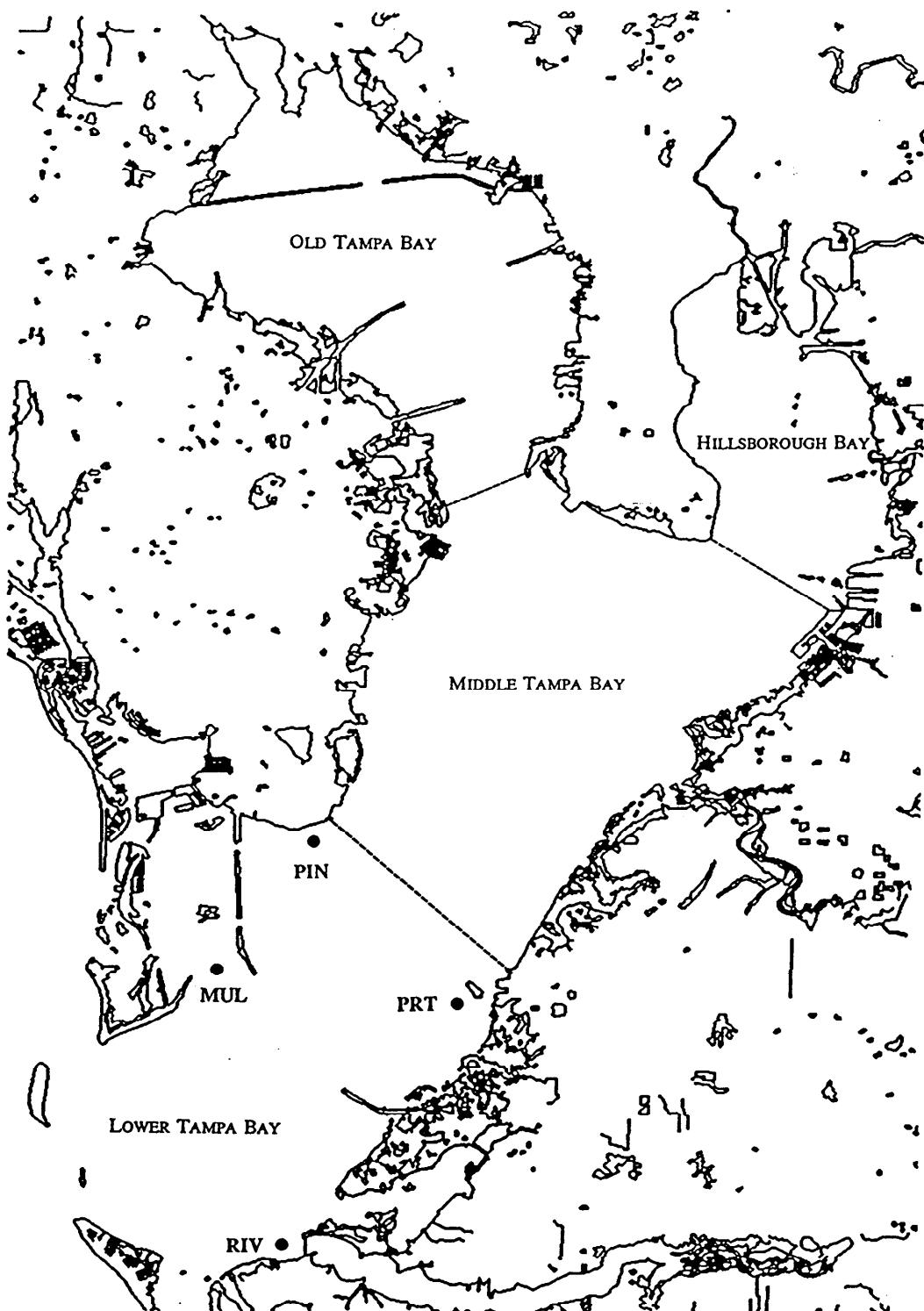


Figure 2. Stations locations and designations for continuous light (PAR) monitoring in Tampa Bay.

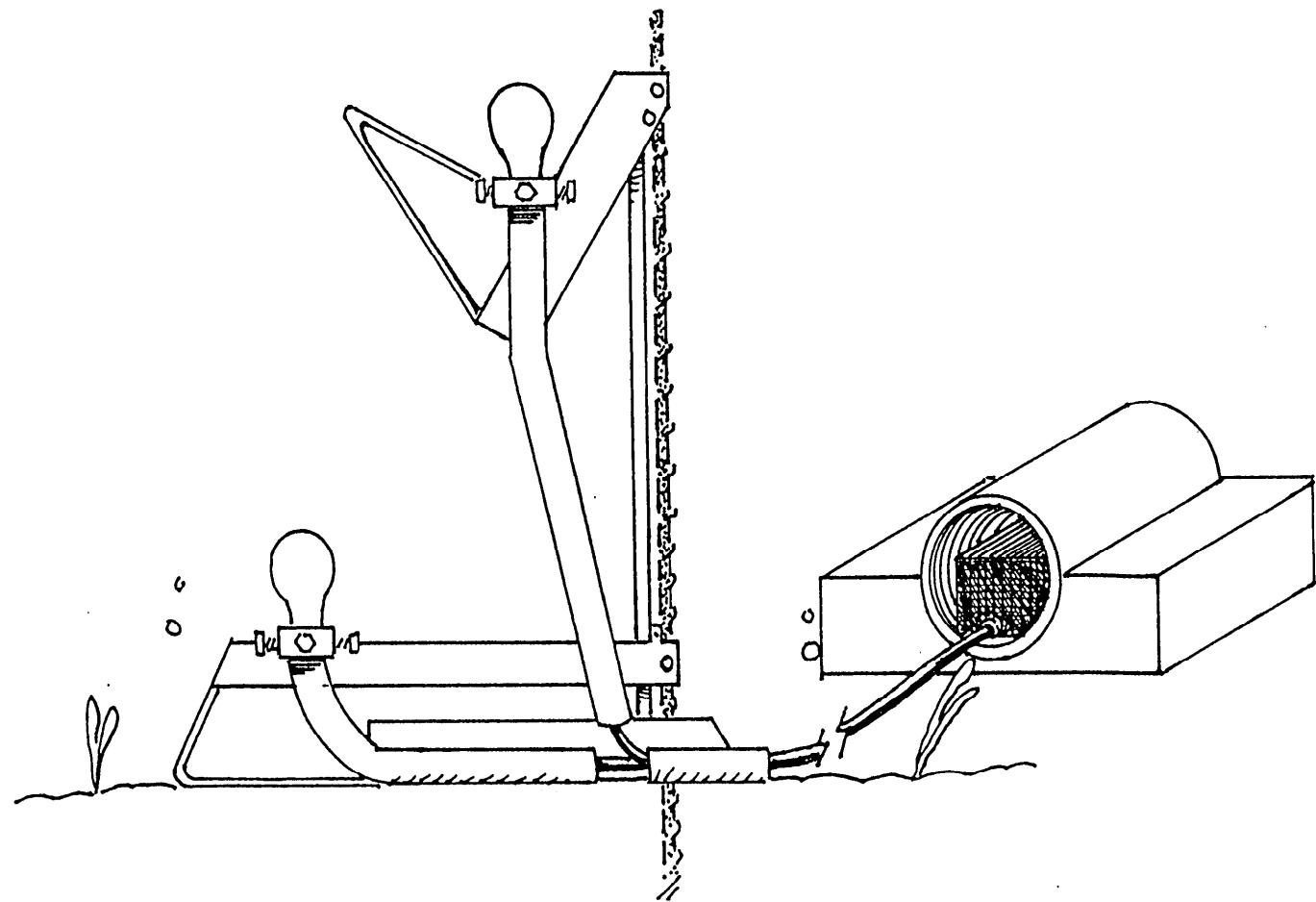


Figure 3. Apparatus for continuous monitoring of underwater PAR in Tampa Bay. Vertical separation of sensors is 0.5 m. Lower sensor is oriented toward the south. Approximate station latitudes are 27.5° N.

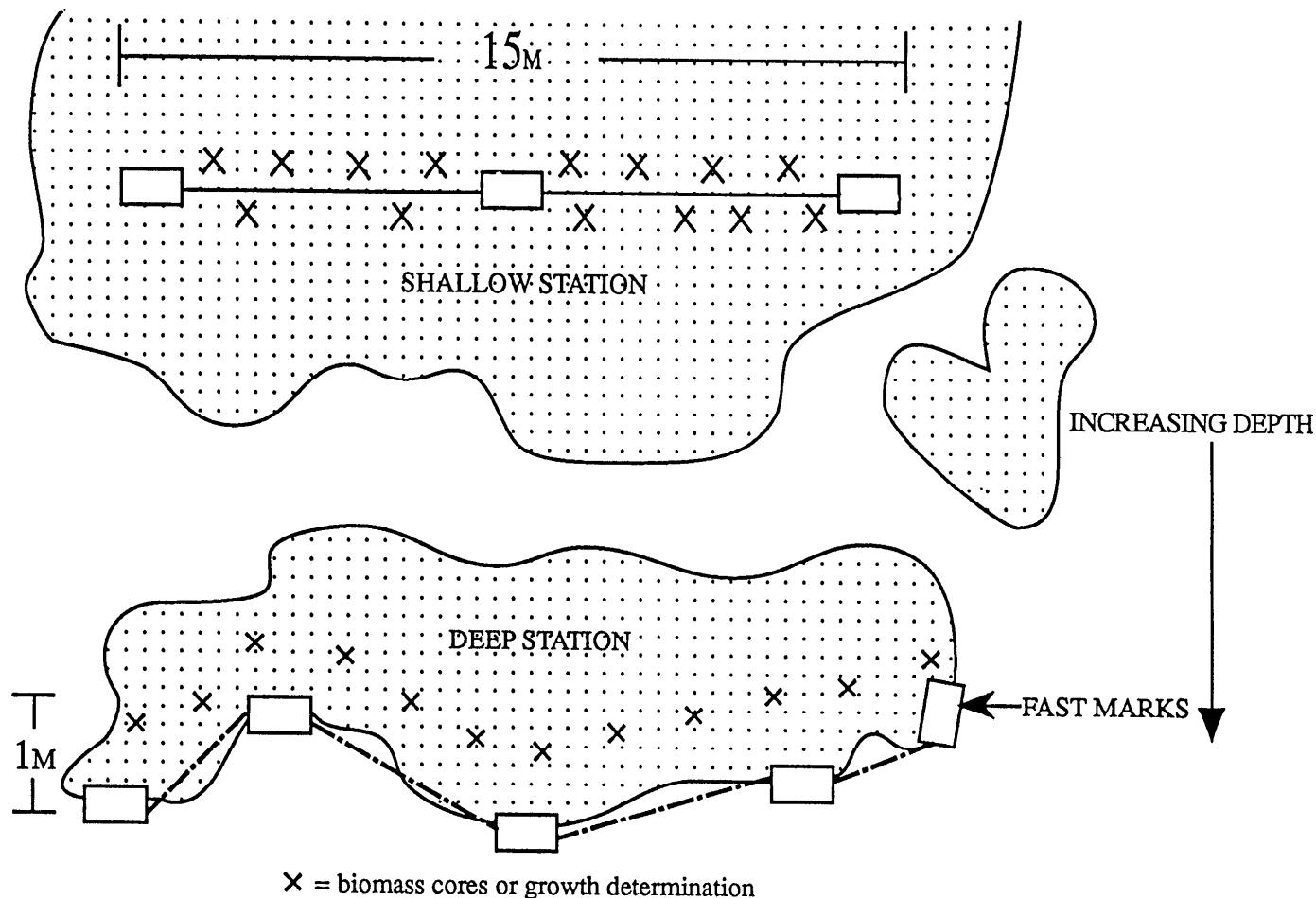


Figure 4. Schematic representation of monitoring sites for *Thalassia* in Tampa Bay, Continuous PAR instrumentation was placed just outside of marked edge at deep station.

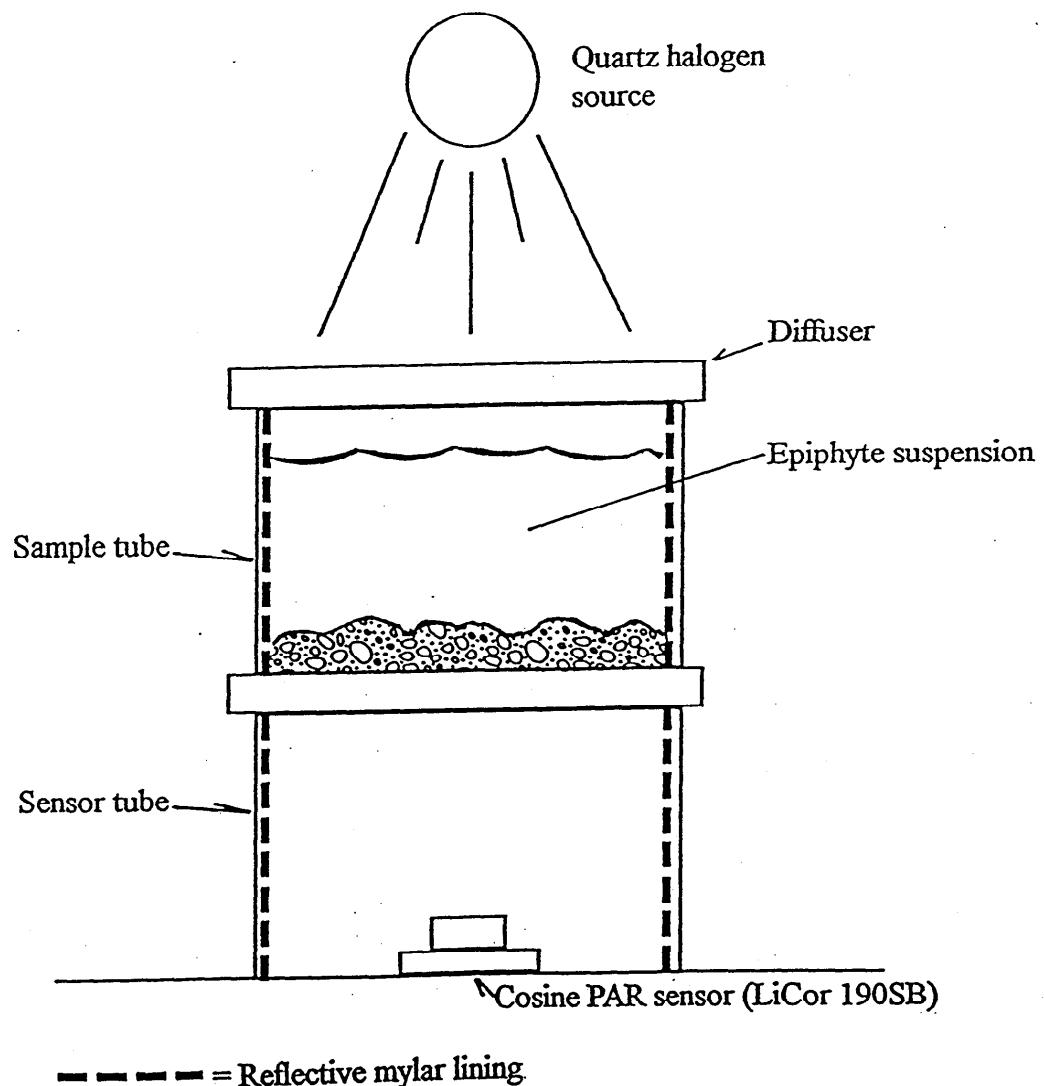


Figure 5. Apparatus for determination of PAR attenuation due to epiphytic material.

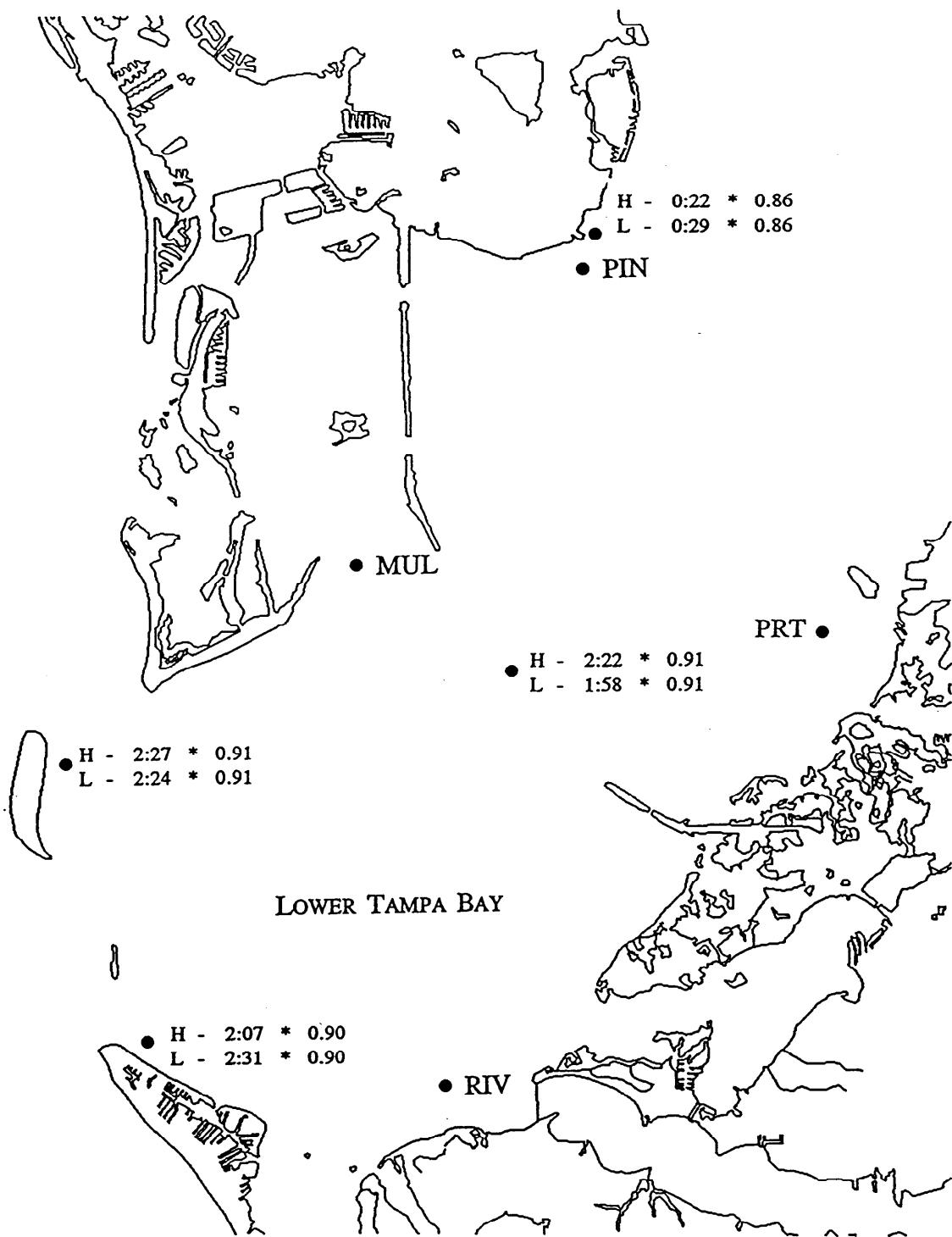


Figure 6. Continuous light monitoring stations and tidal differences available for Tampa Bay.

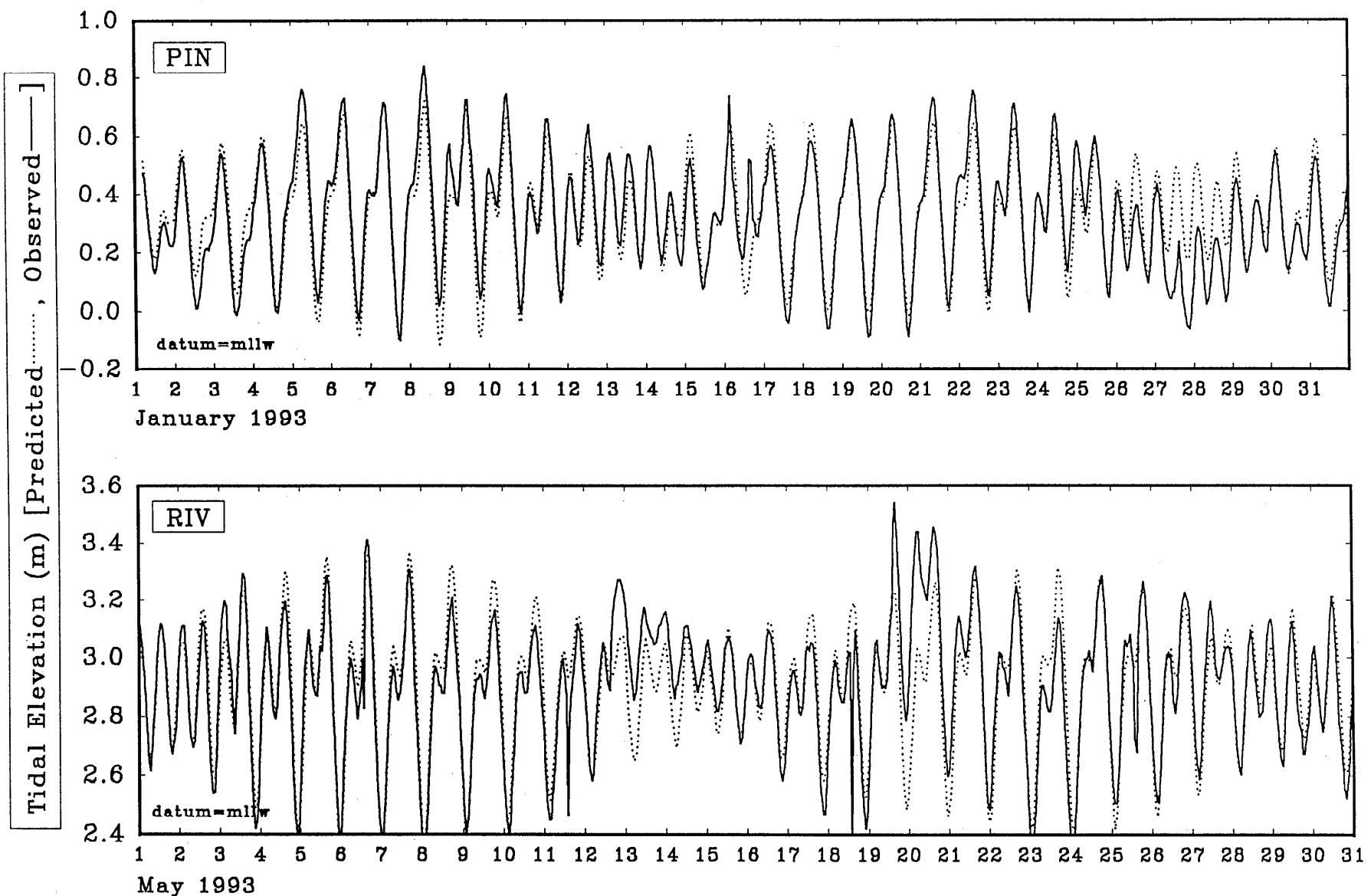


Figure 7. Examples of the correspondence of predicted tidal heights with observed initiating data for PIN and RIV.

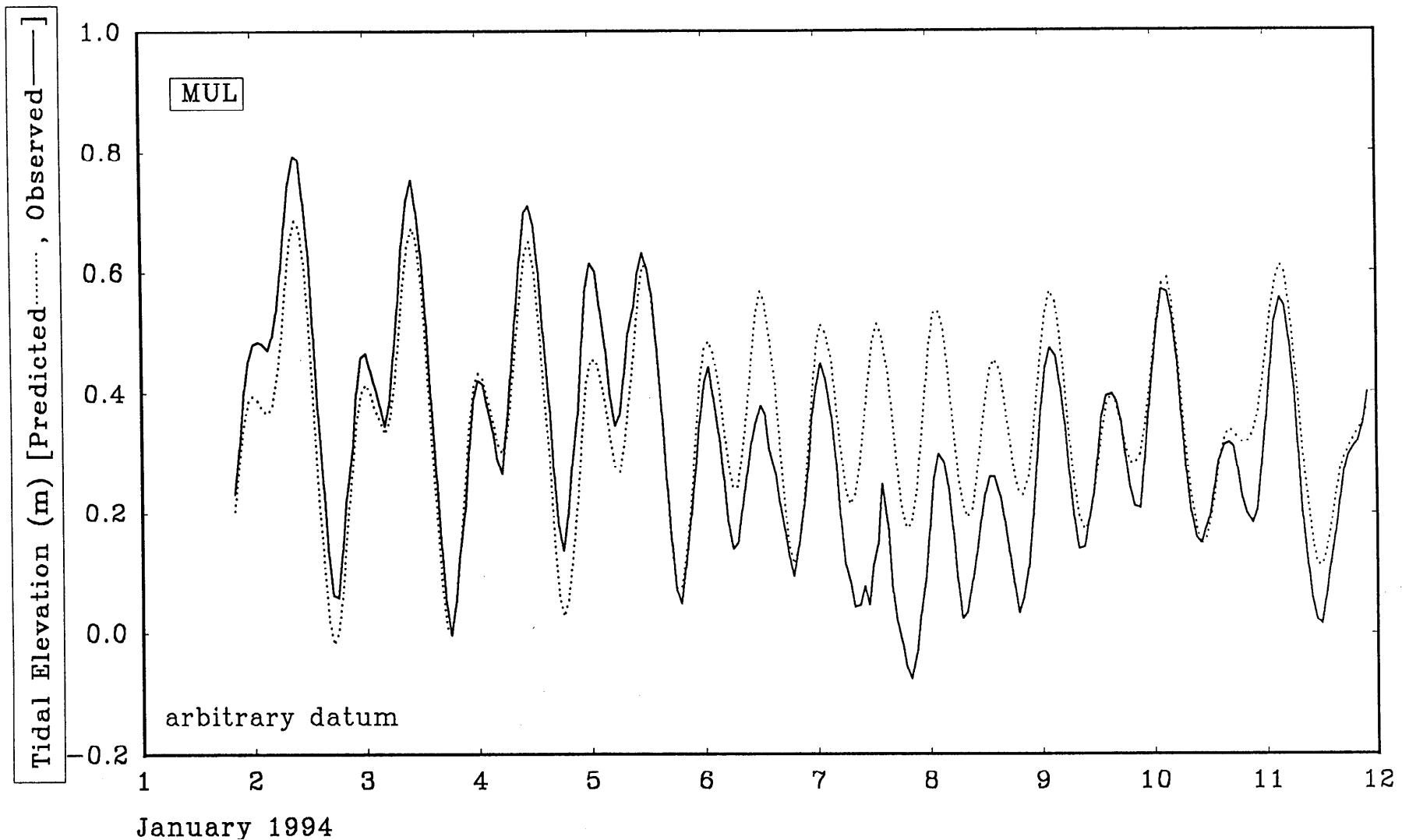


Figure 8. Example of the effects of weather on water levels and the resultant overprediction of tidal heights during winter storms with northerly winds.

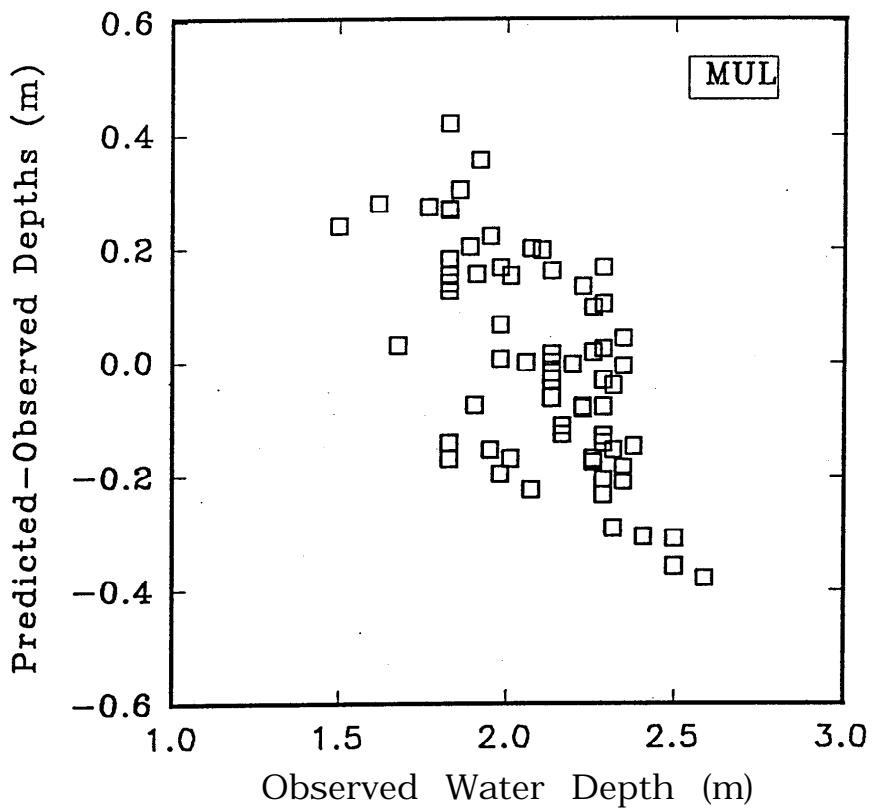
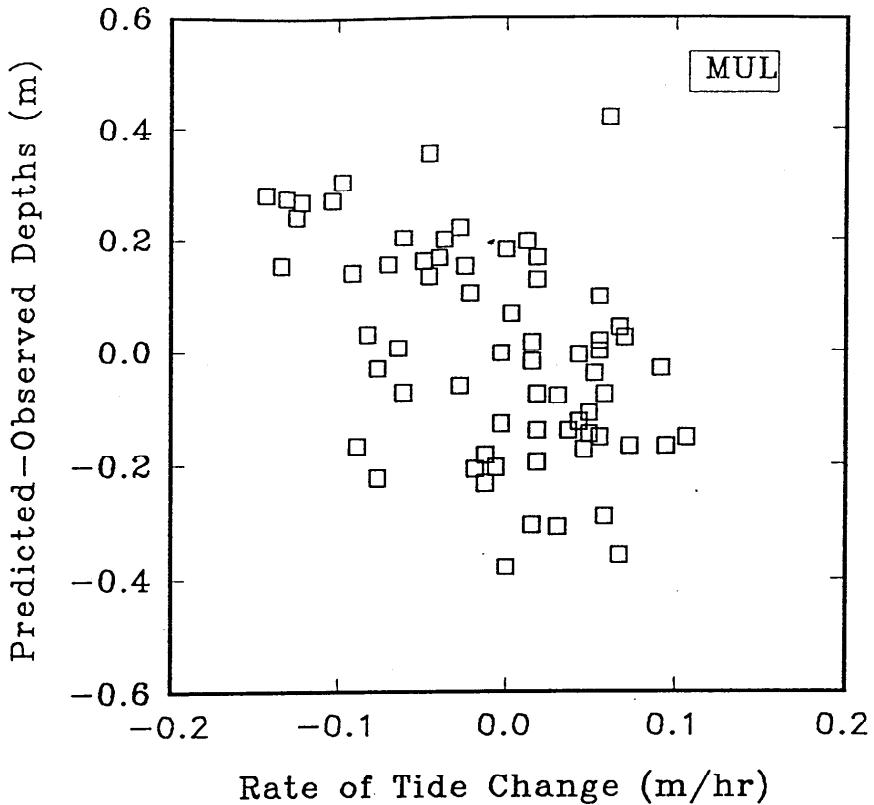


Figure 9. Residuals from tidally varying water depth predictions. Upper figure (a) illustrates lack of dependence on rate of change in predicted tide (*i.e.*, no significant phase shifts between observed and predicted data). Lower figure (b) illustrates the weather-induced deviations of observed depths from predicted tides.

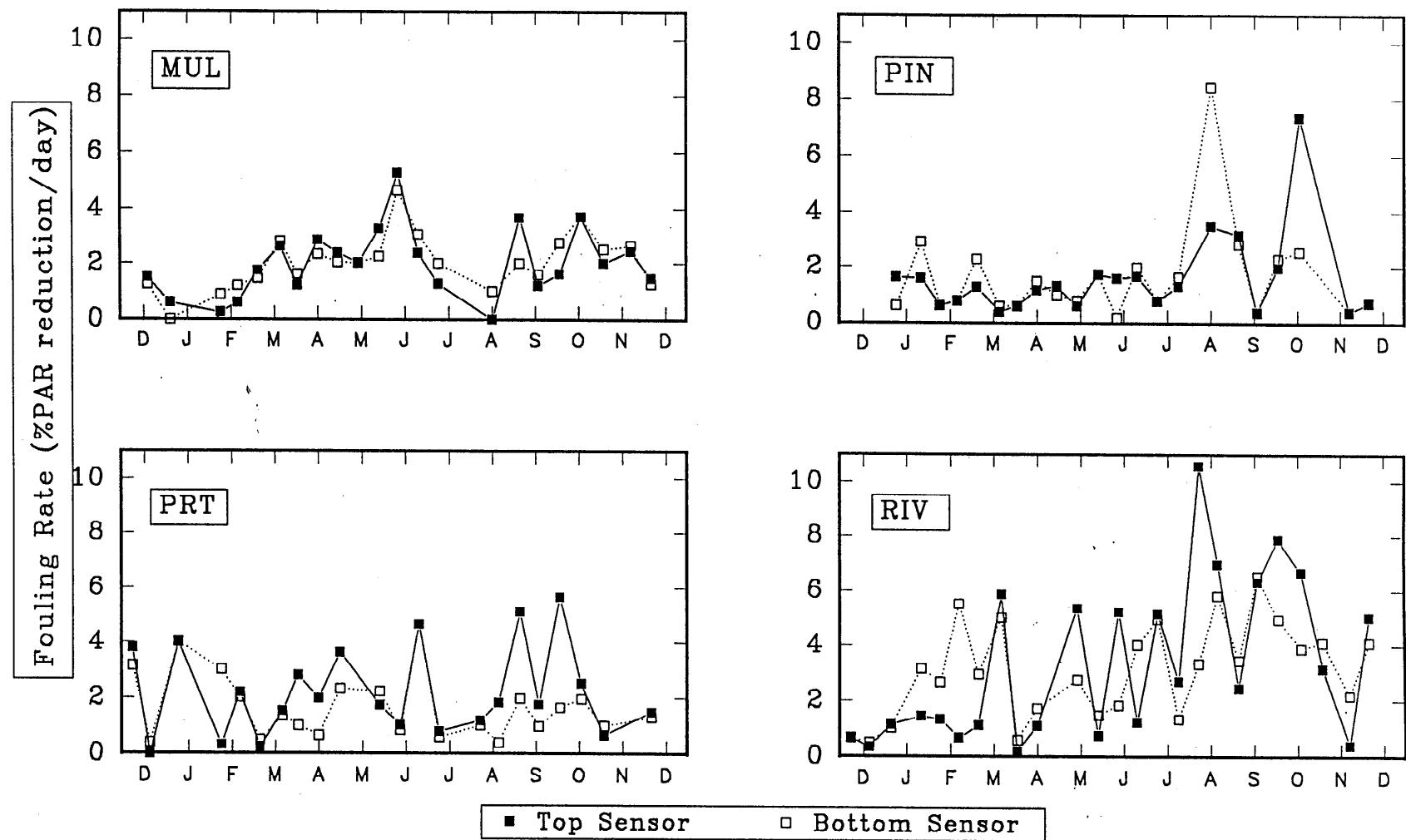


Figure 10. Fouling rates (percent PAR reduction day⁻¹) measured on PAR sensors and used for correction of recorded PAR data.

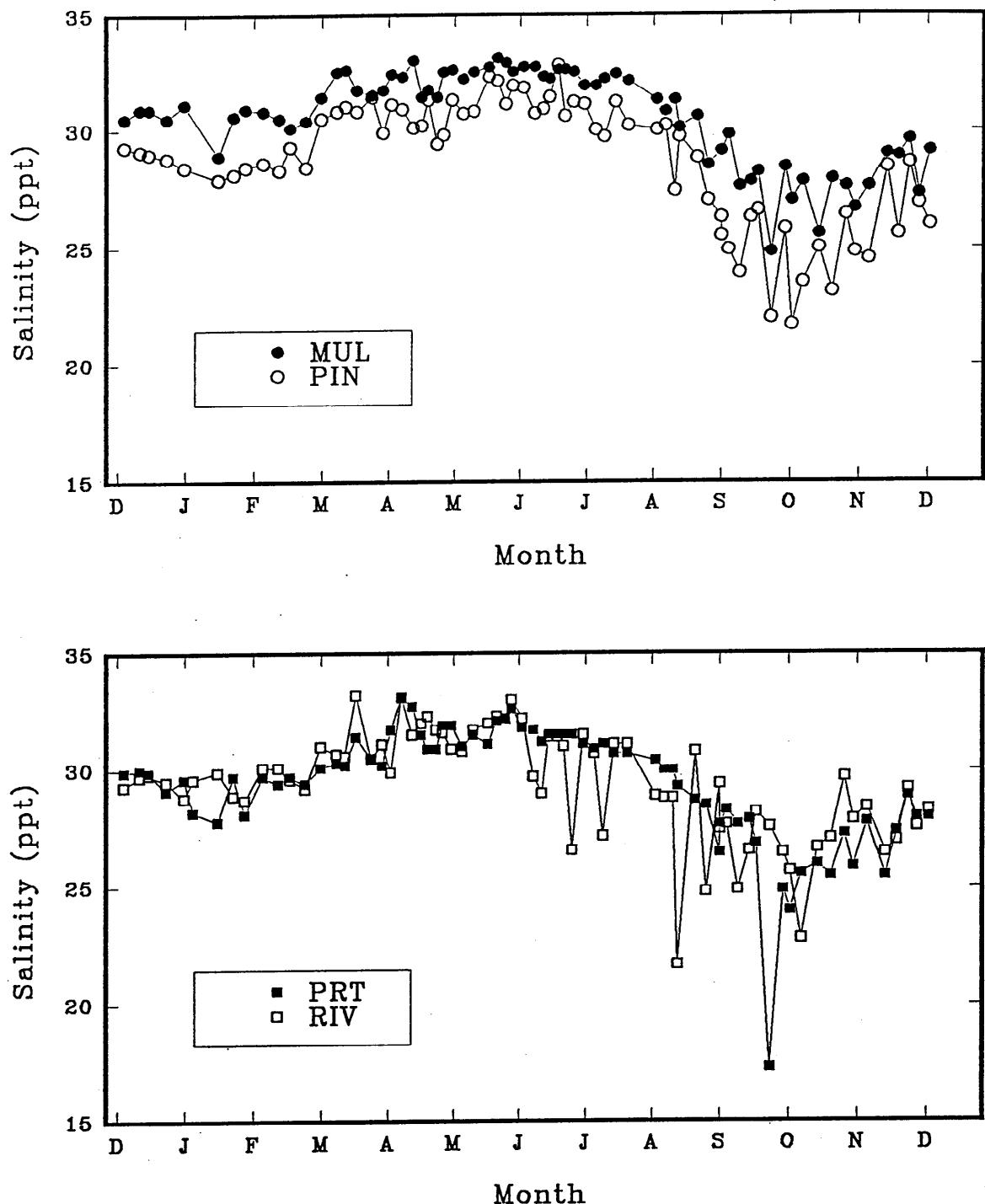


Figure 11. Annual patterns of salinity at continuous PAR monitoring stations. Samples were typically surface grabs samples.

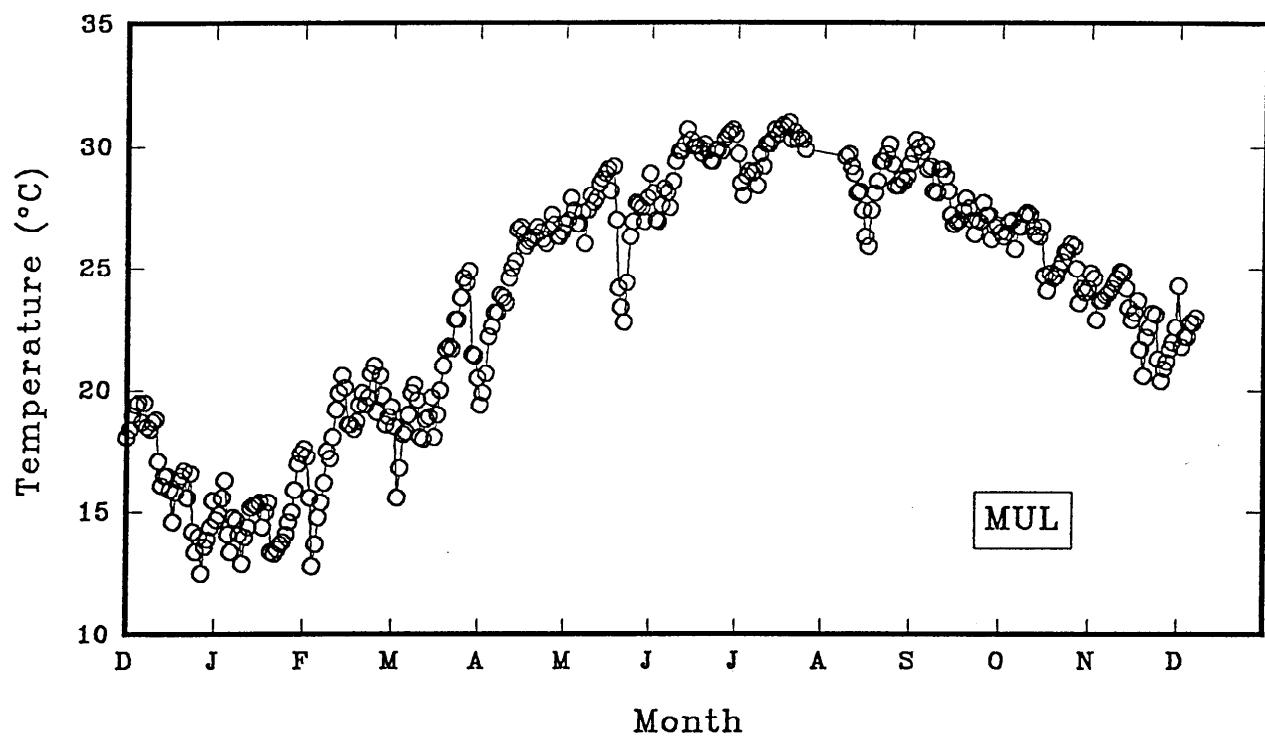


Figure 12. Annual patterns of temperature at continuous PAR monitoring stations. Data illustrated are for MUL.

SECCHI DEPTH ANNUAL AVERAGE

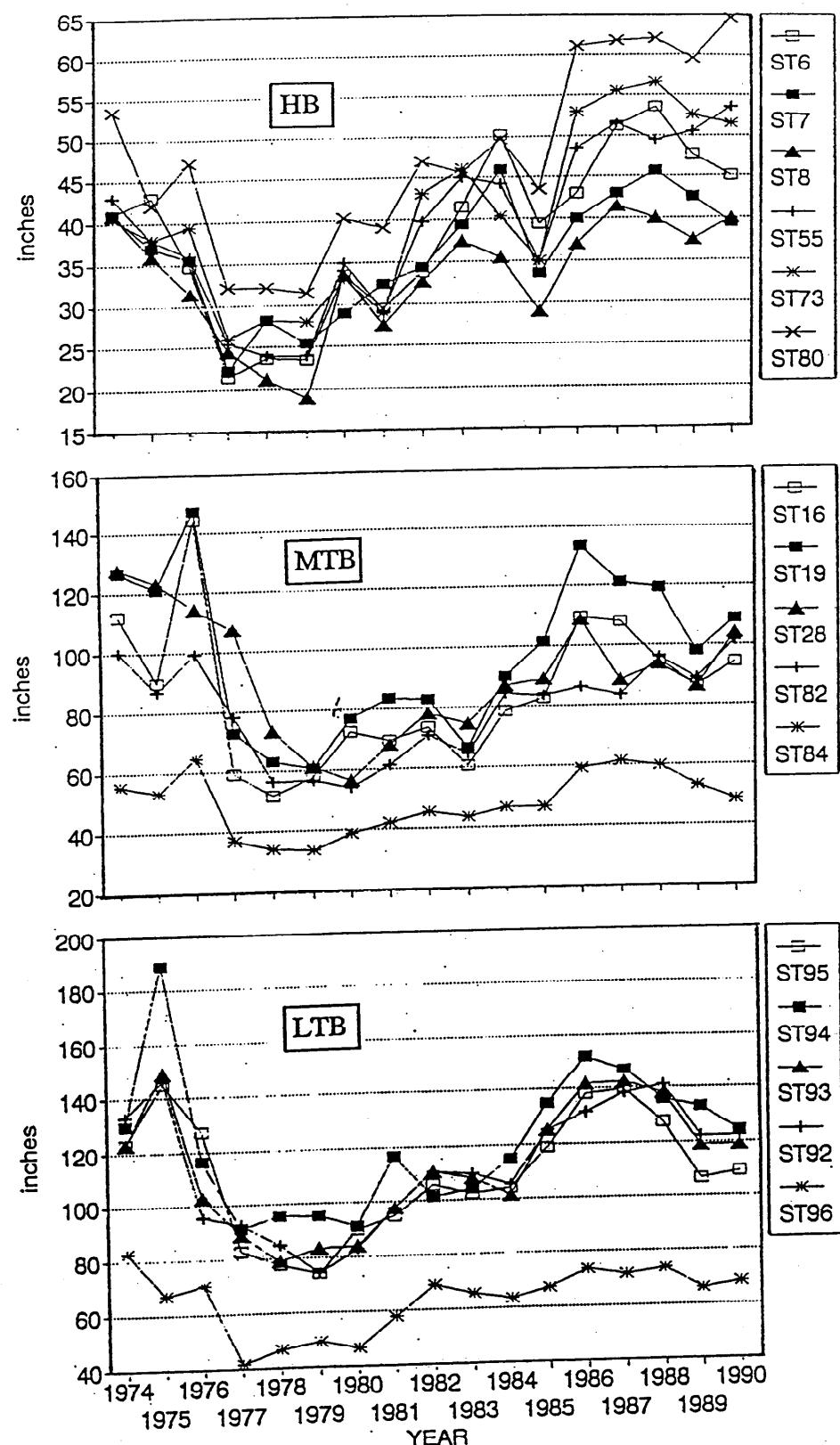


Figure 13. Annual average Secchi depths for Hillsborough County Environmental Protection stations in Hillsborough (HB), Middle Tampa (MTB), and Lower Tampa Bays (LTB) (Source: King, 1992).

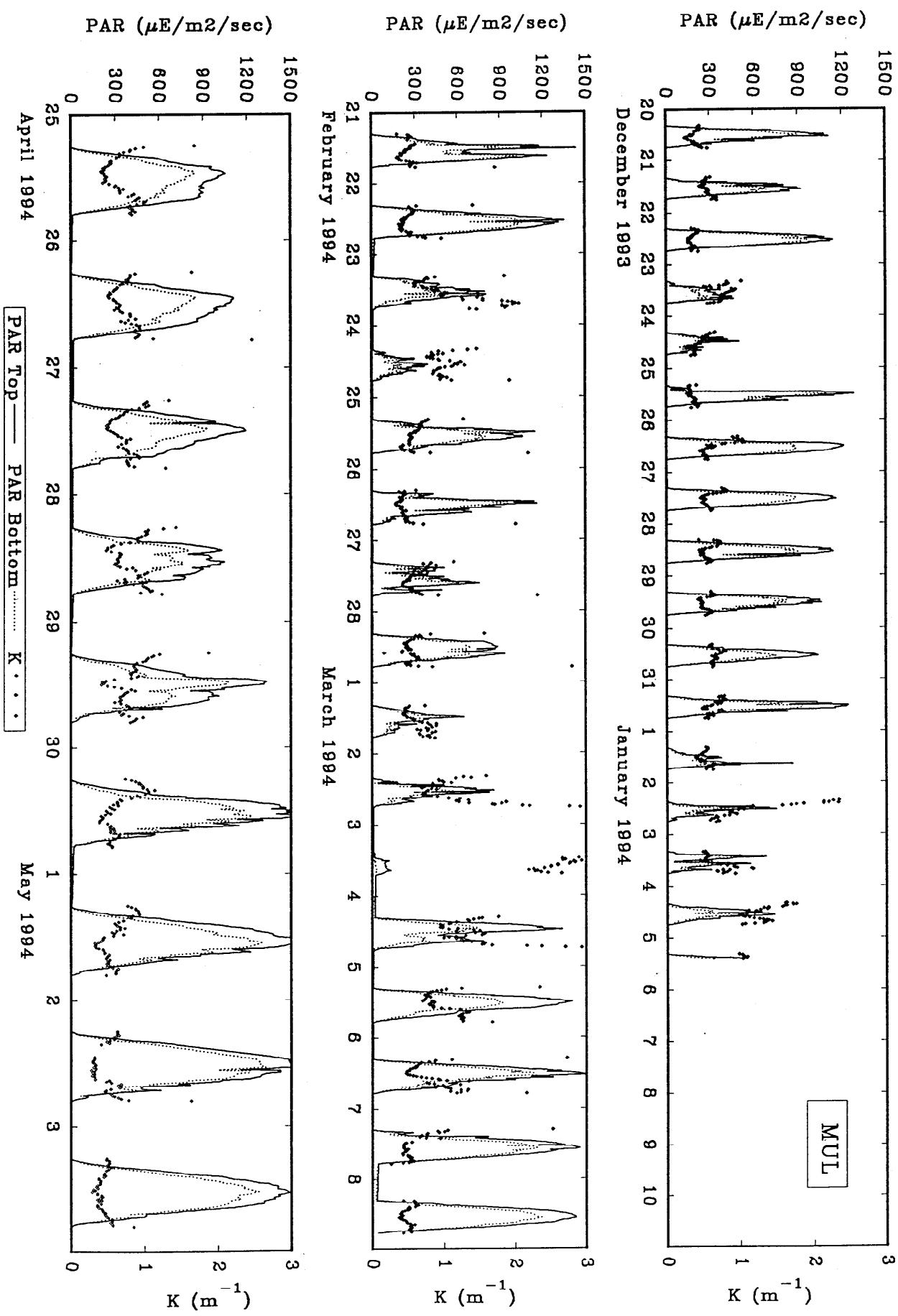


Figure 14. Observed water column PAR for top and bottom sensors and calculated attenuation coefficients at the maximum depth limits of *Thalassia* beds during the periods between seagrass blade marking and recovery. Illustrated for the MUL deep station.

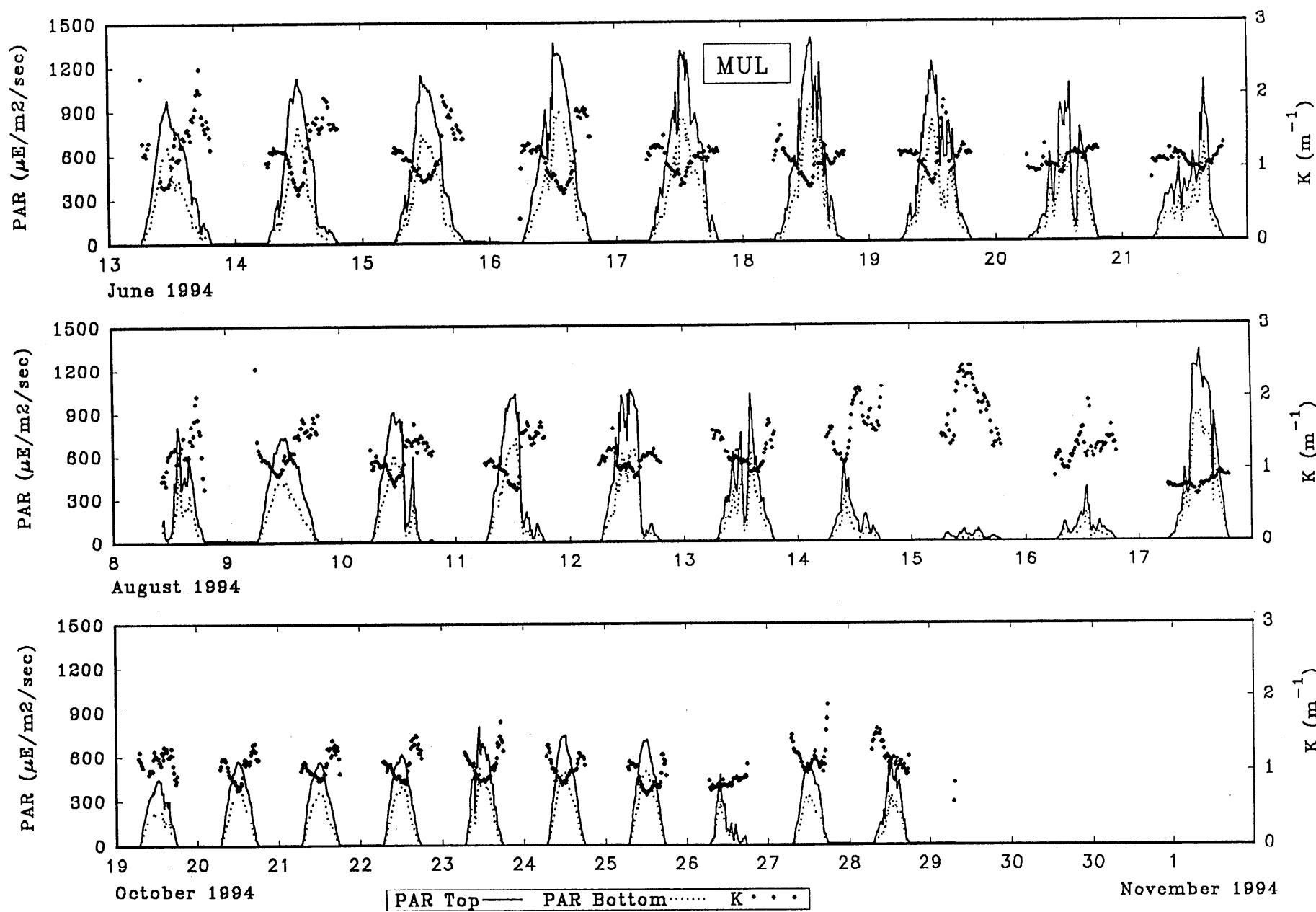


Figure 14. Continued.

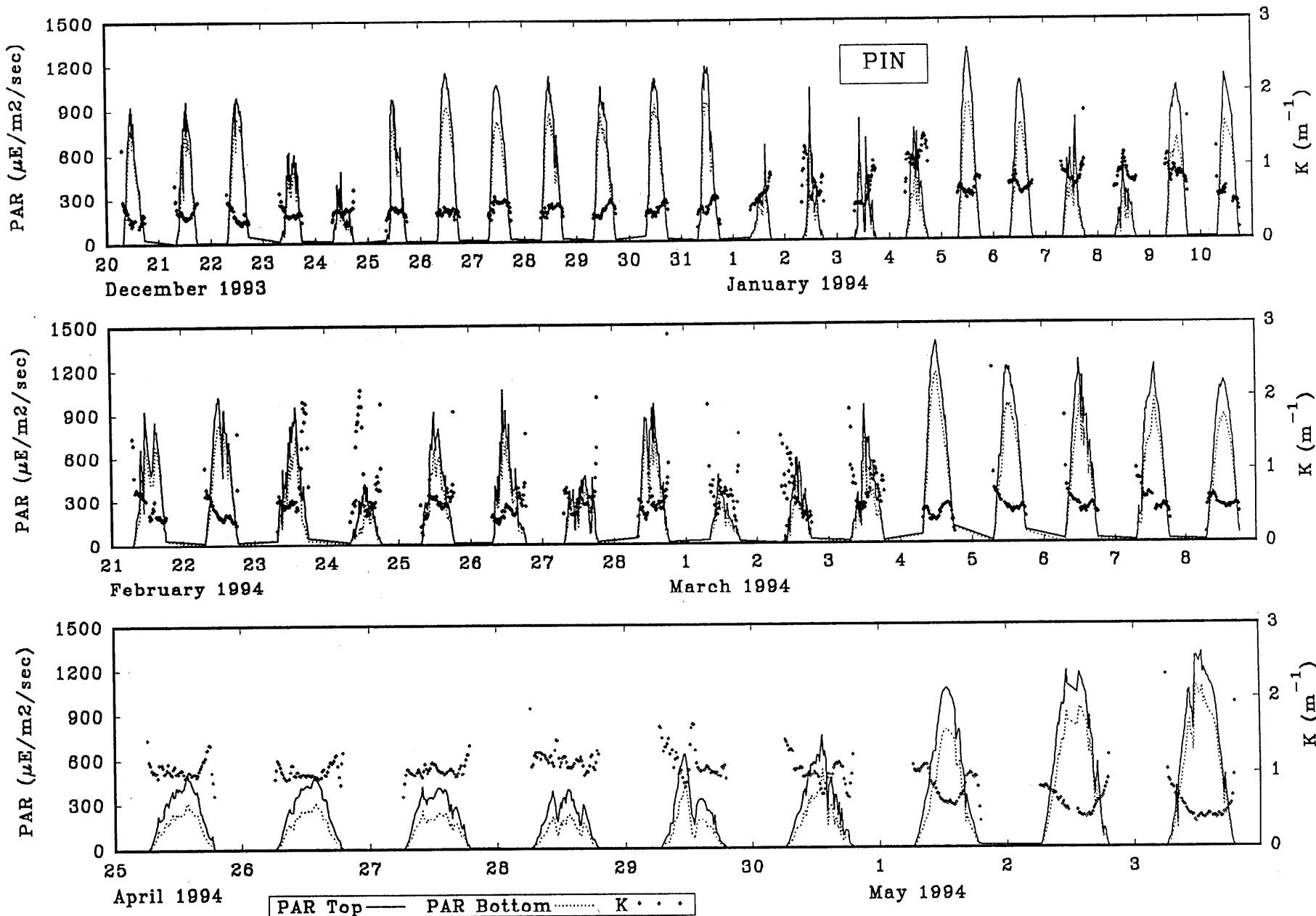


Figure 15. Observed water column PAR for top and bottom sensors and calculated attenuation coefficients at the maximum depth limits of *Thalassia* beds during the periods between seagrass blade marking and recovery. Illustrated for the PIN deep station.

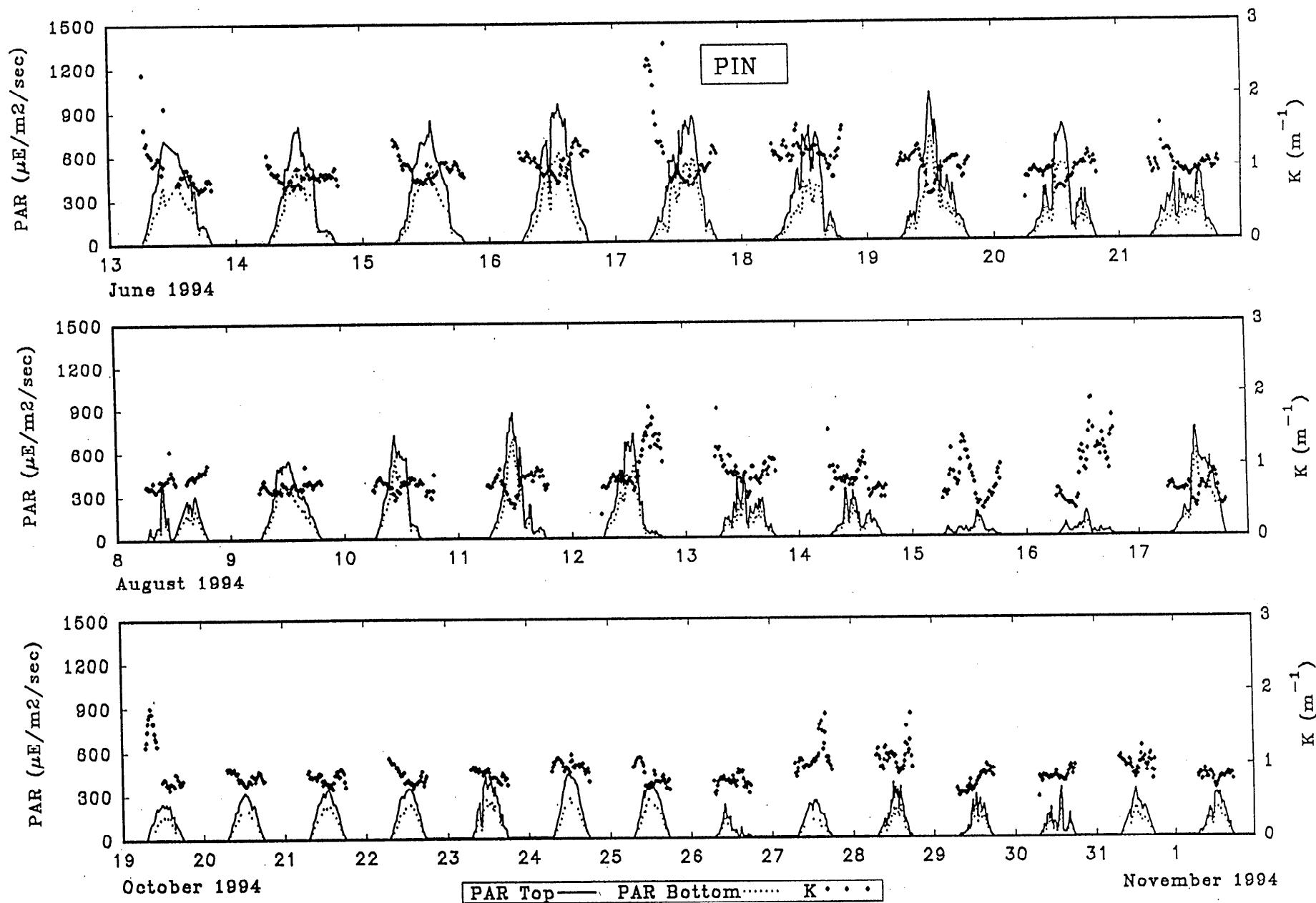


Figure 15. Continued.

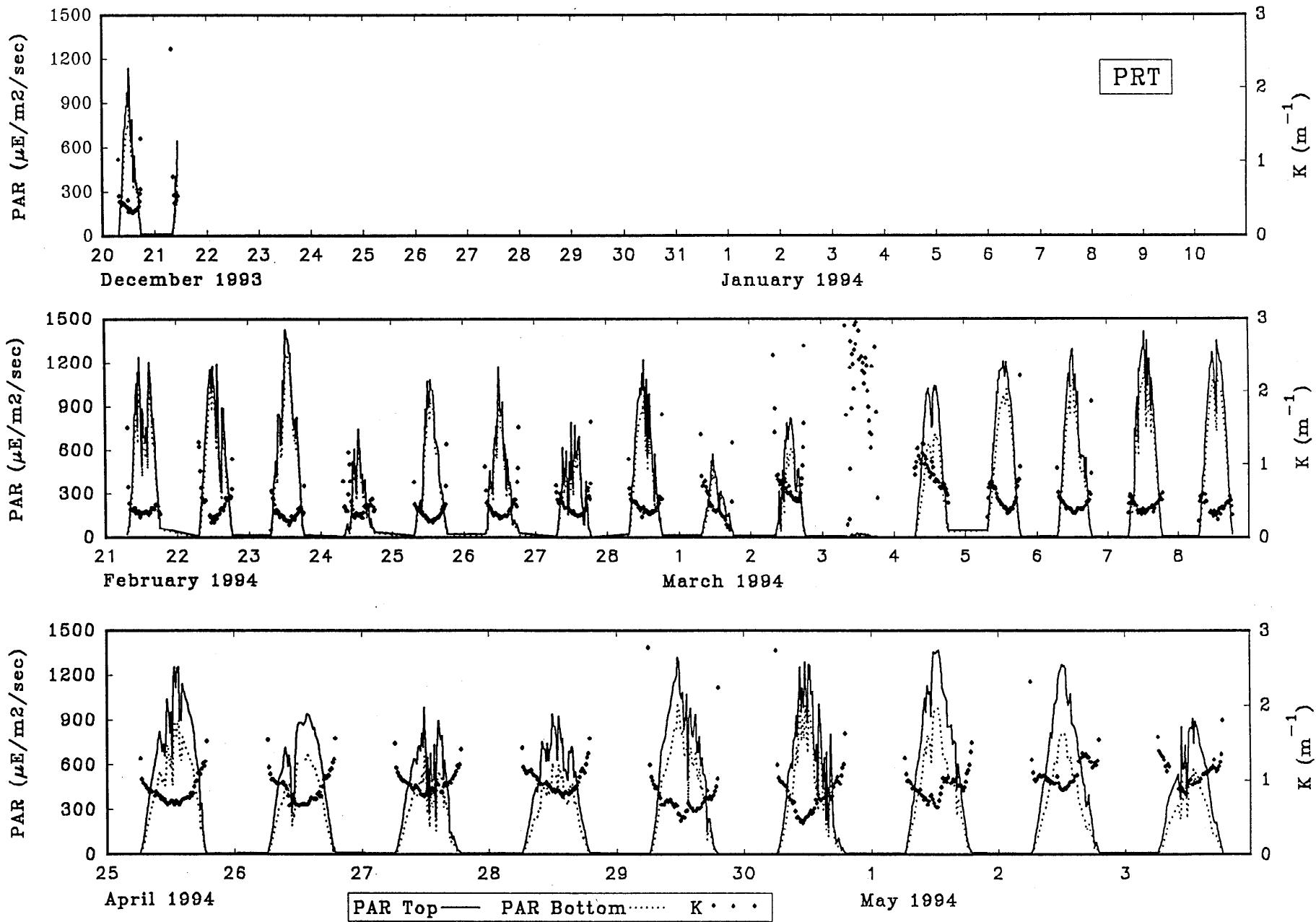


Figure 16. Observed water column PAR for top and bottom sensors and calculated attenuation coefficients at the maximum depth limits of *Thalassia* beds during the periods between seagrass blade marking and recovery. Illustrated for the PRT deep station.

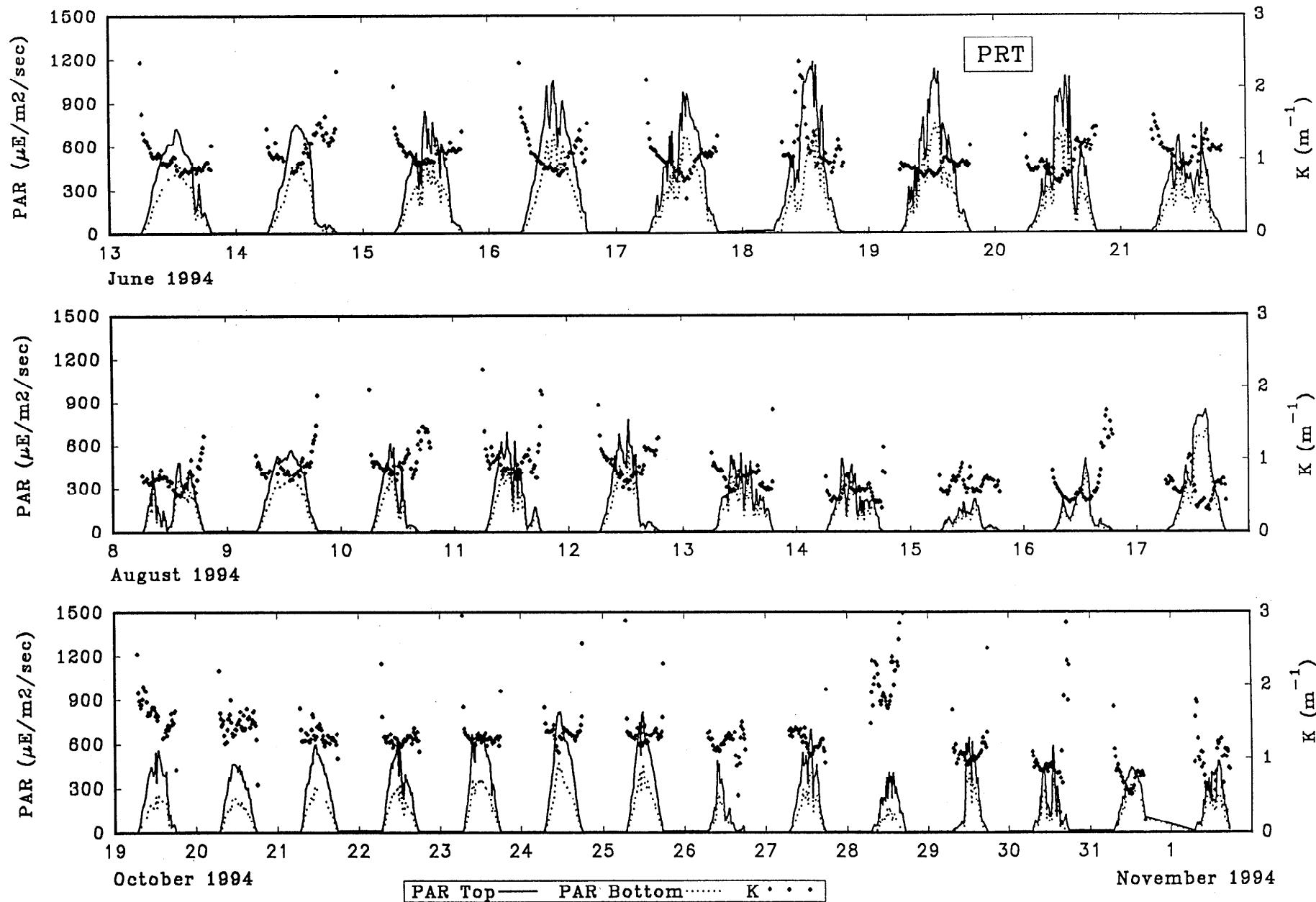


Figure 16. Continued.

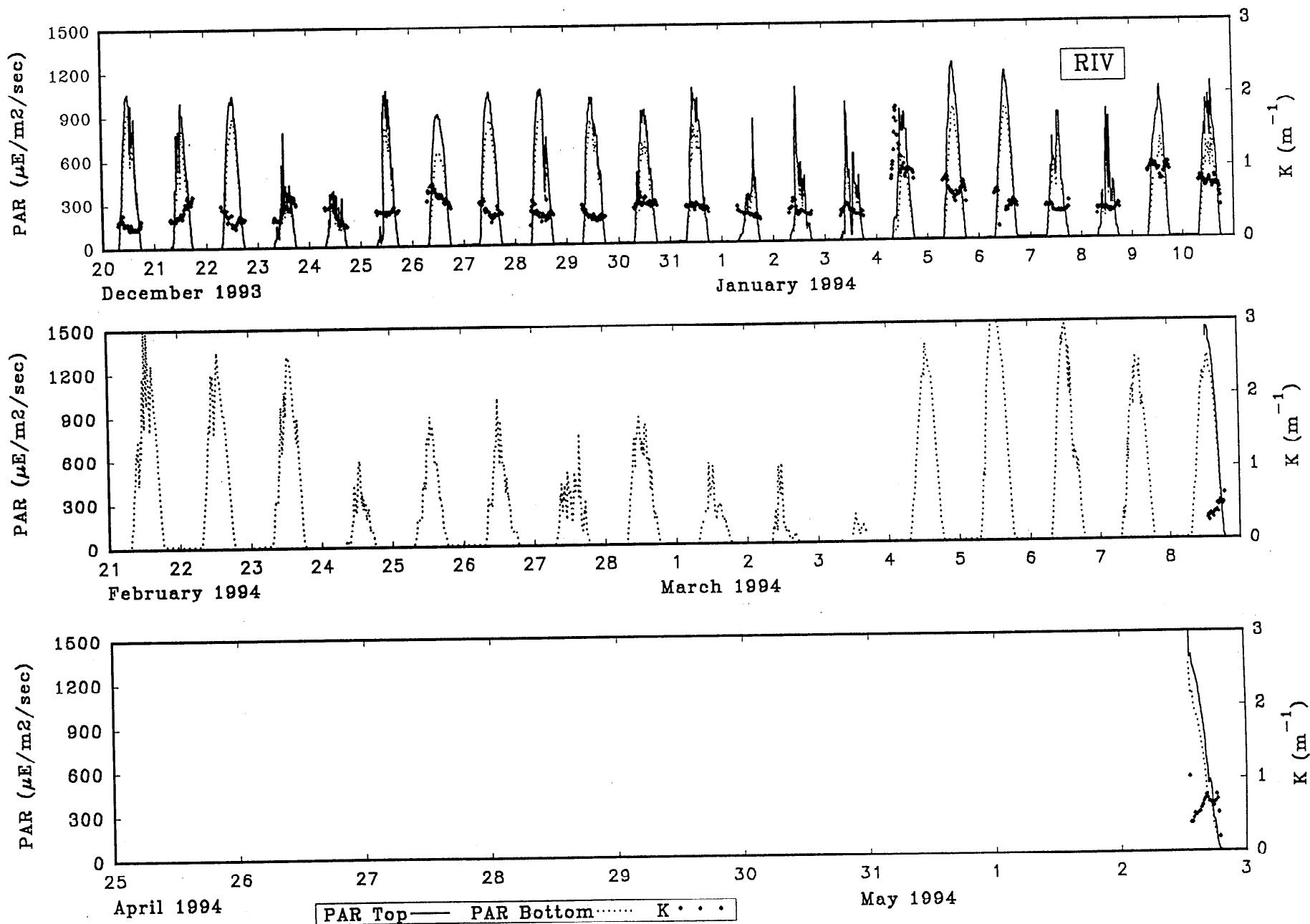


Figure 17. Observed water column PAR for top and bottom sensors and calculated attenuation coefficients at the maximum depth limits of *Thalassia* beds during the periods between seagrass blade marking and recovery. Illustrated for the RIV deep station.

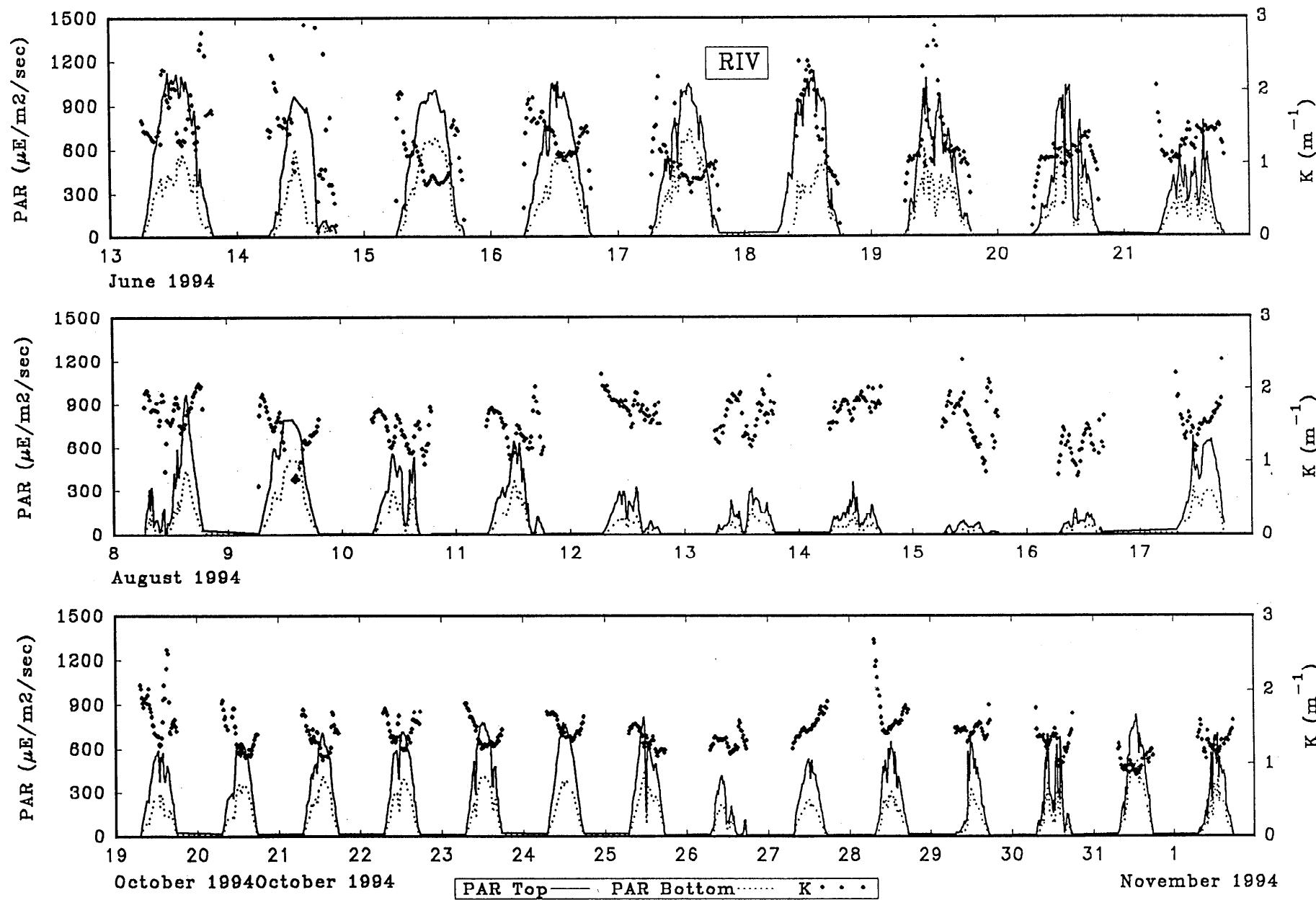


Figure 17. Continued.

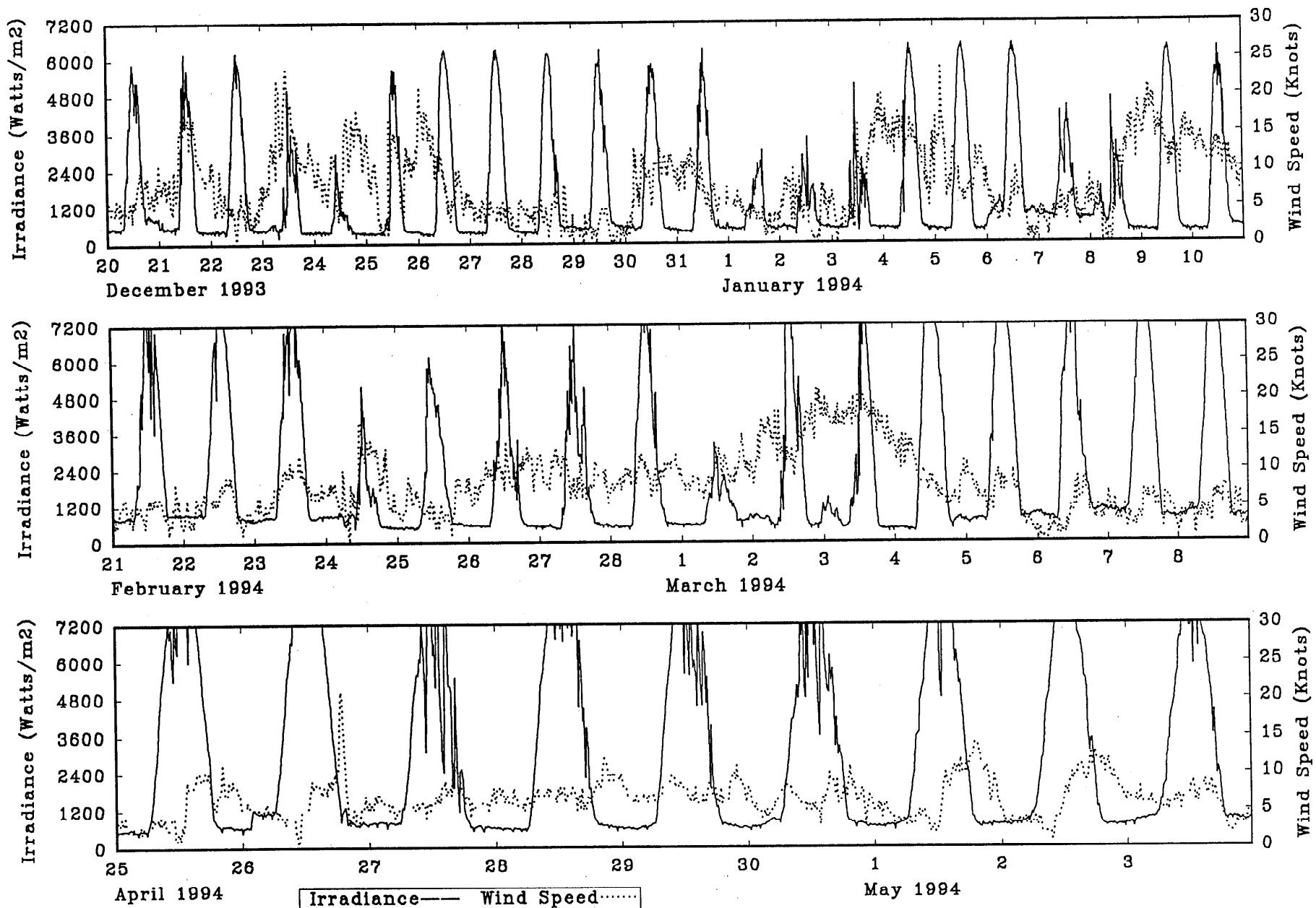


Figure 18. Incident (in air) irradiance (solid line) and wind speed (broken line) at Mote Marine Laboratory, (~35 km to the south of Tampa Bay), during the periods between seagrass blade marking and recovery.

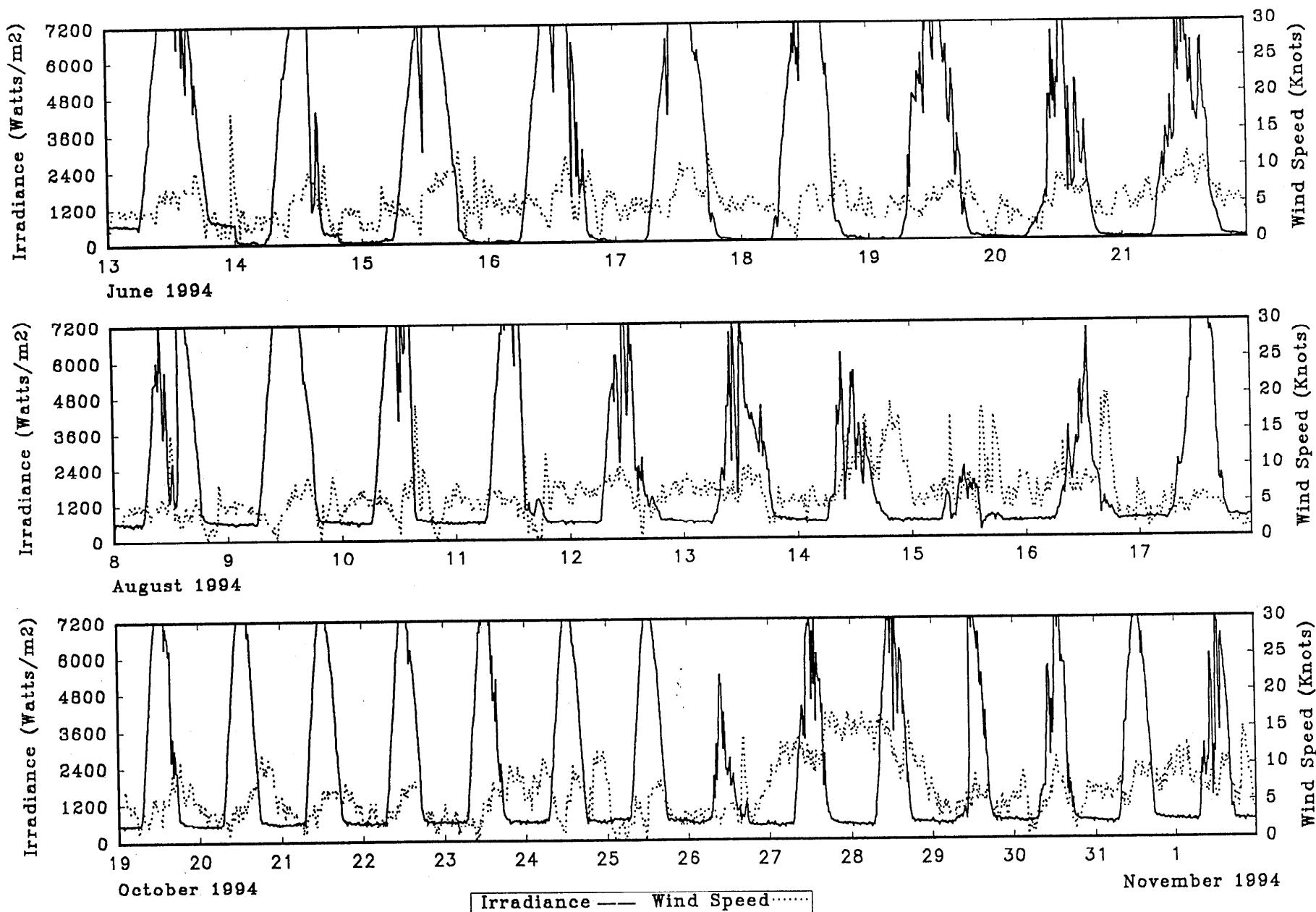


Figure 18. Continued.

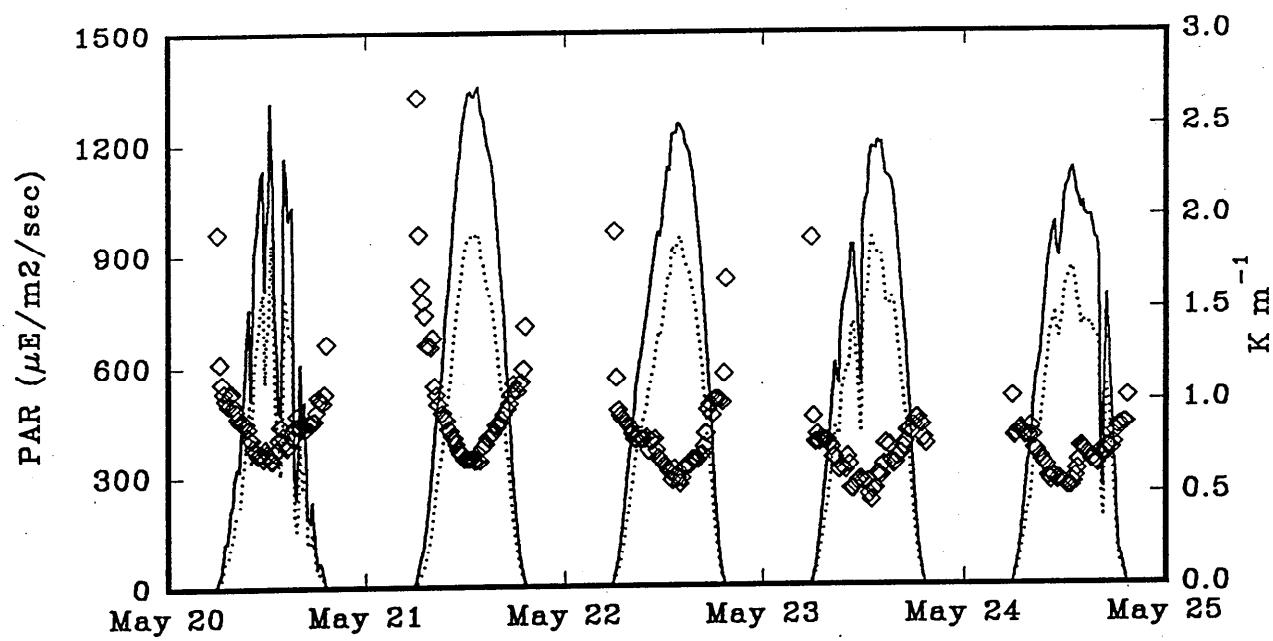
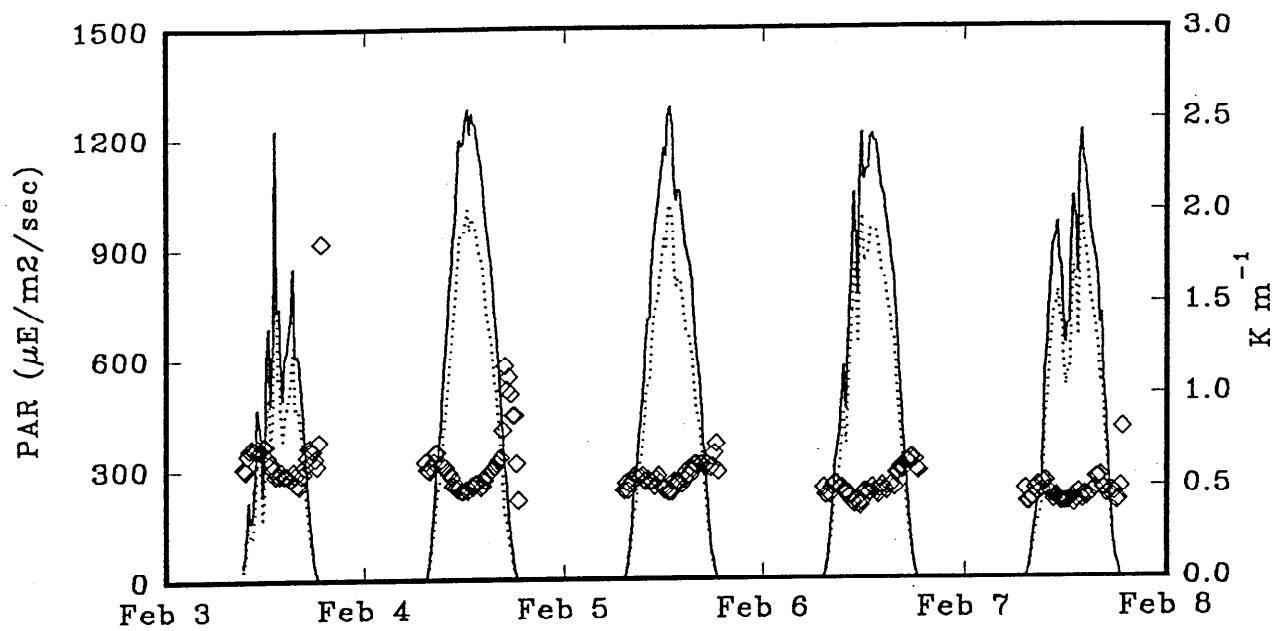


Figure 19. Diurnal variations in attenuation coefficient (diamonds) produced by varying solar elevation. Annual variations in the magnitude of diurnal variation.

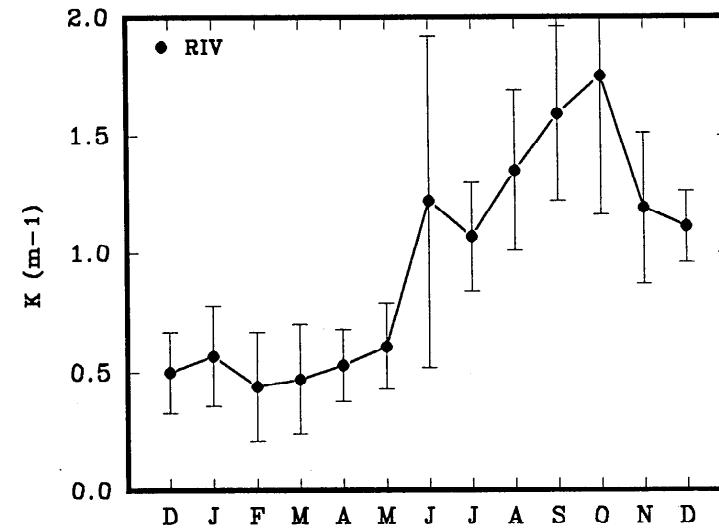
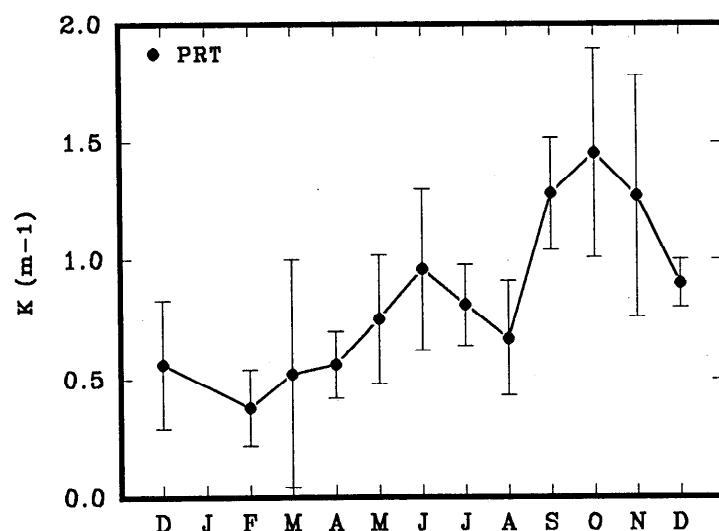
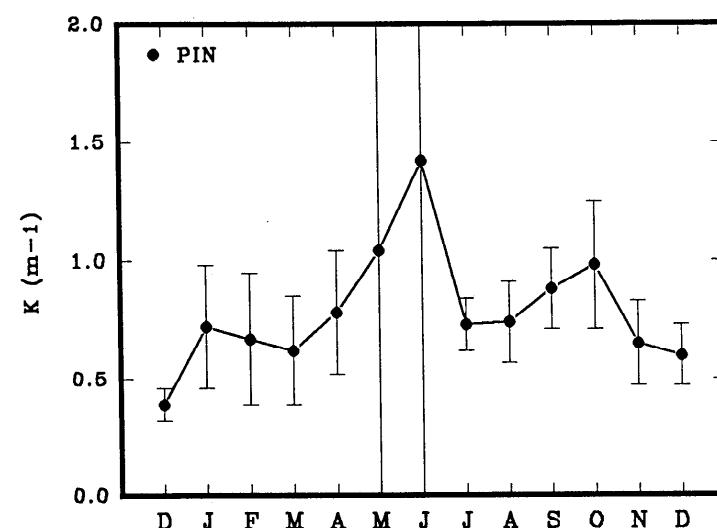
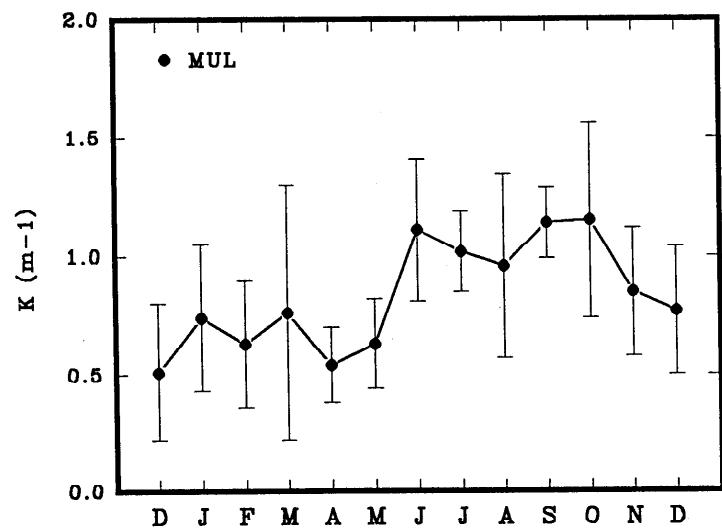


Figure 20. Attenuation coefficients (K_0) determined between 1000-1400 hours at Tampa Bay continuous light stations, monthly means and standard deviations by station.

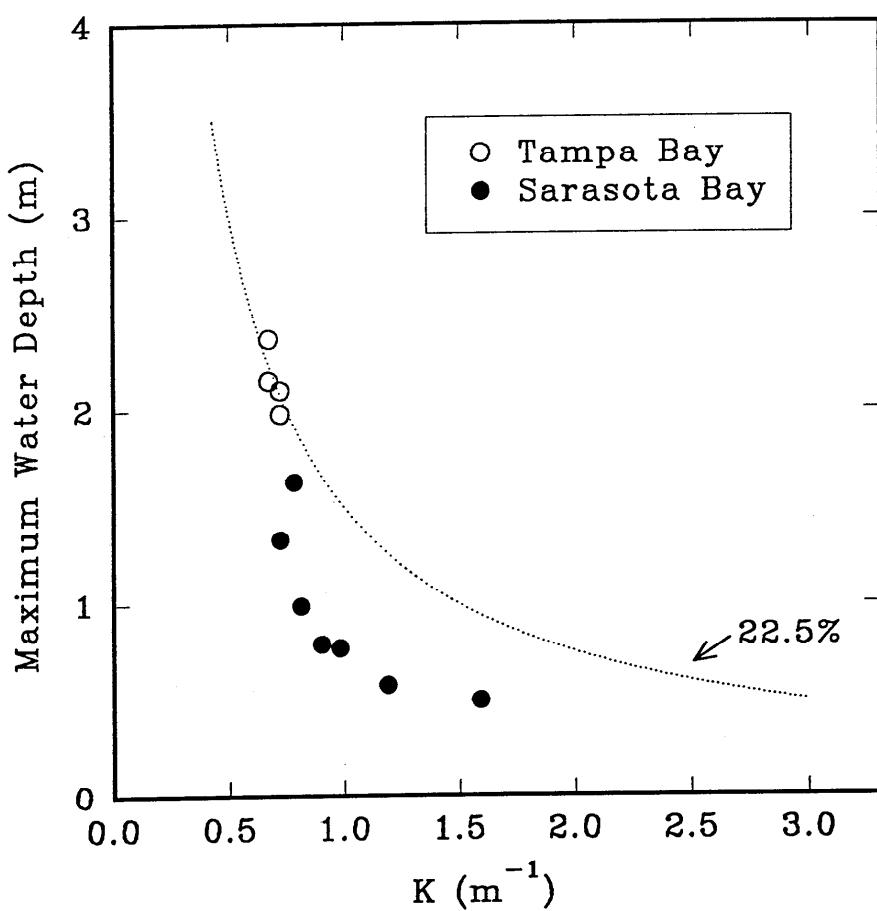


Figure 21. Maximum depth limits as a function of water column attenuation (K_0) alone. Comparison of maximum depth limits of seagrass beds in Tampa and Sarasota Bays with the annual average isolume of 22.5% as received by Tampa Bay stations. Sarasota Bay data include data from both ***Thalassia*** and ***Halodule*** beds. The effects of epiphytic attenuation are not included.

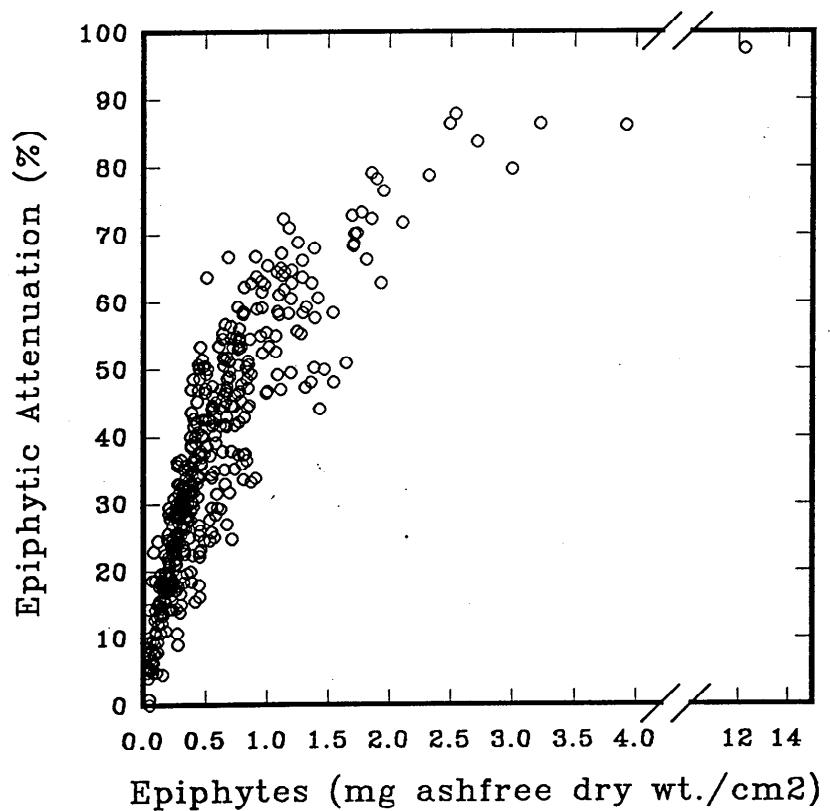
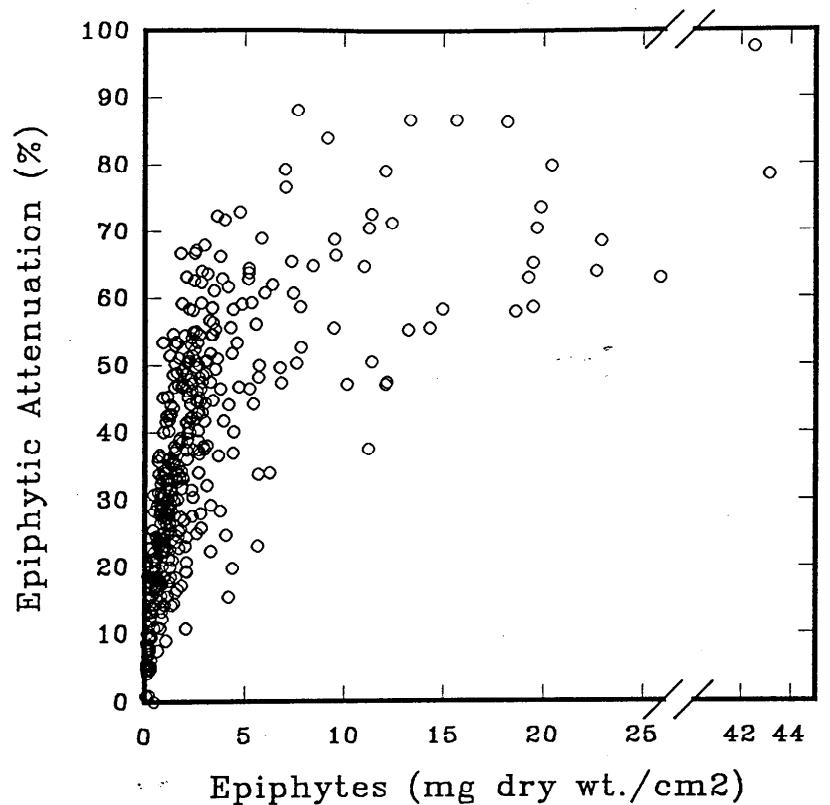


Figure 22. Relationship of epiphytic loads, both total and ash-free mgdwt cm⁻², with PAR attenuation determined as an integrated whole shoot value.

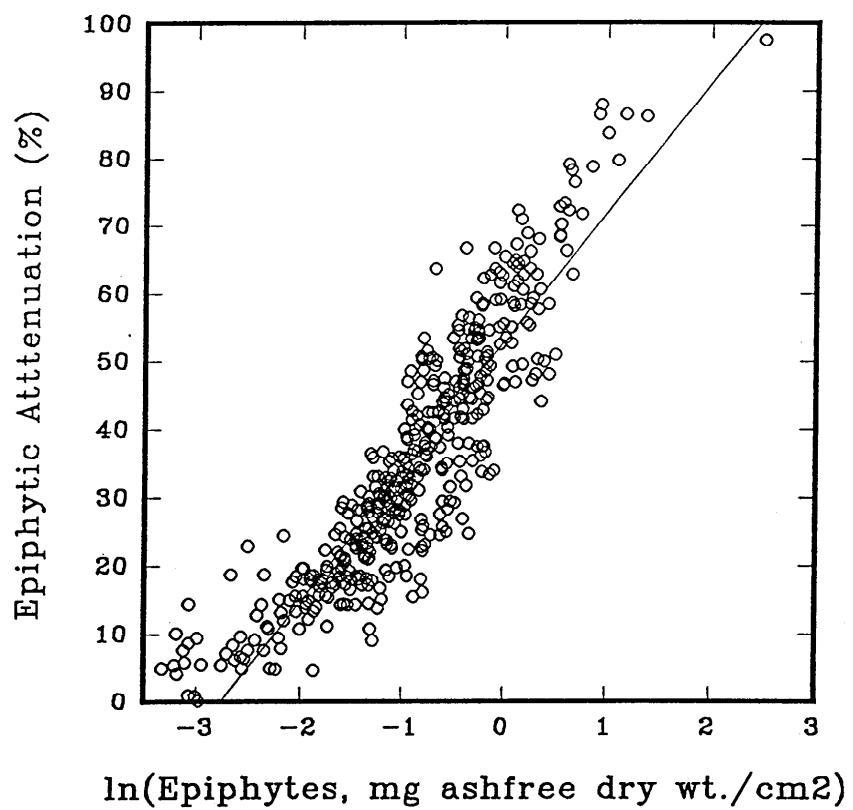


Figure 23. Empirical relationship of epiphytic load (mg of ash-free mgdwt cm^{-2}) to integrated whole shoot PAR attenuation.

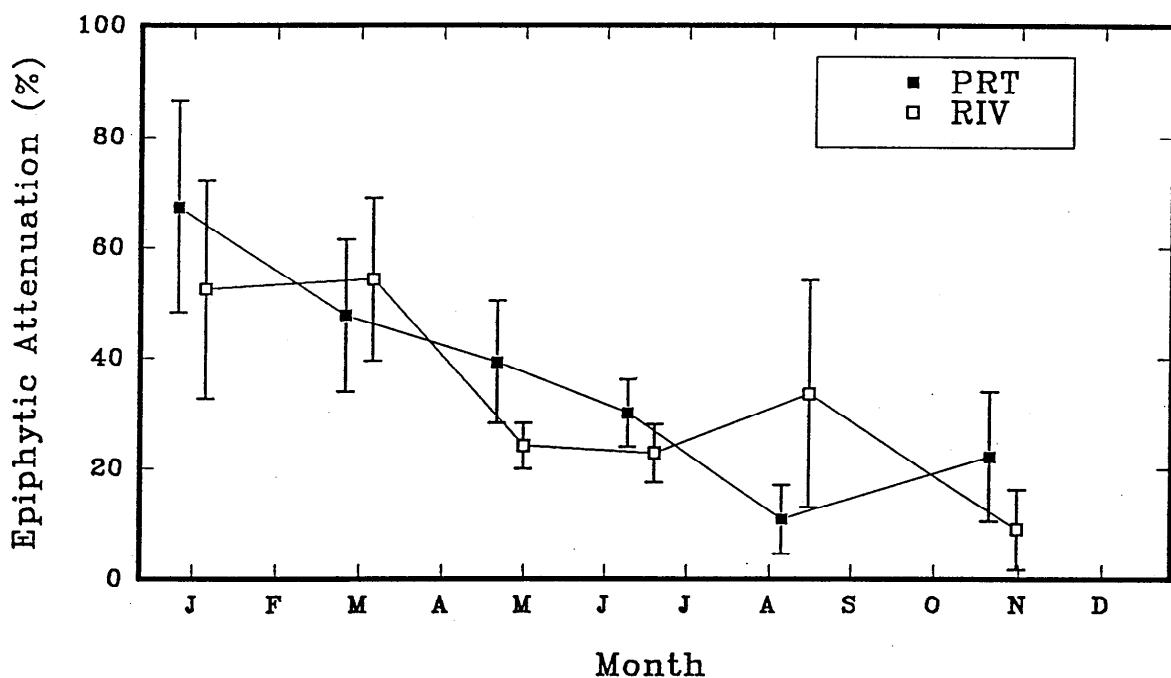
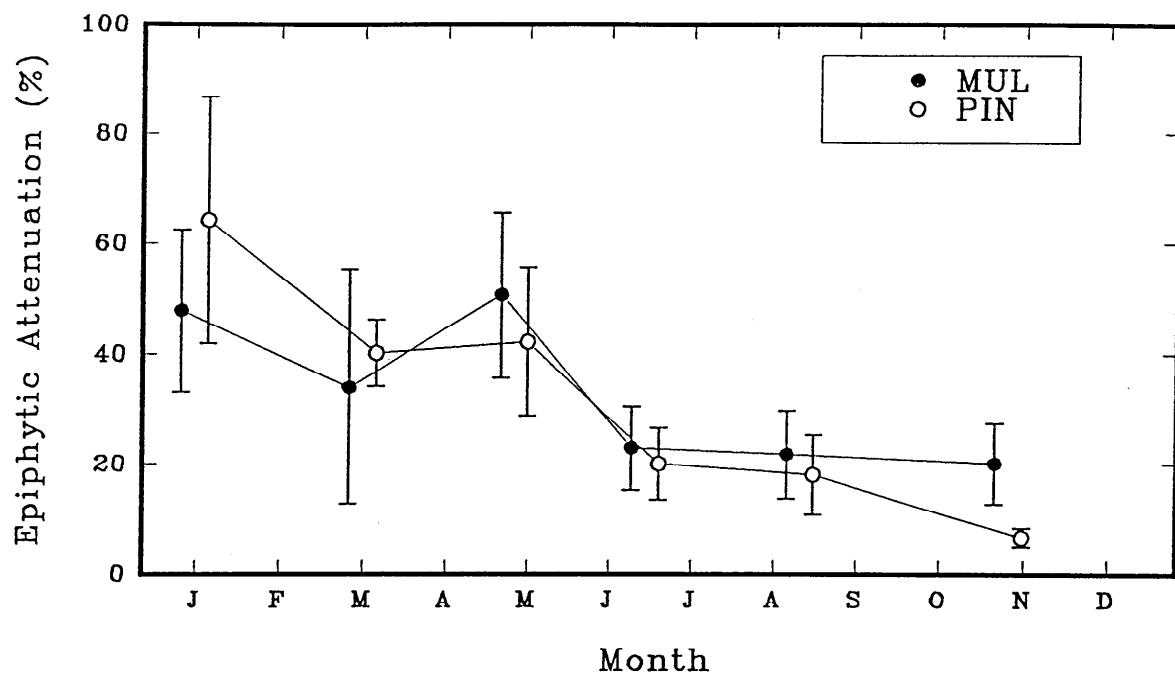


Figure 24. Seasonal patterns of epiphytic attenuation at maximum depth limits of *Thalassia* beds in Tampa Bay

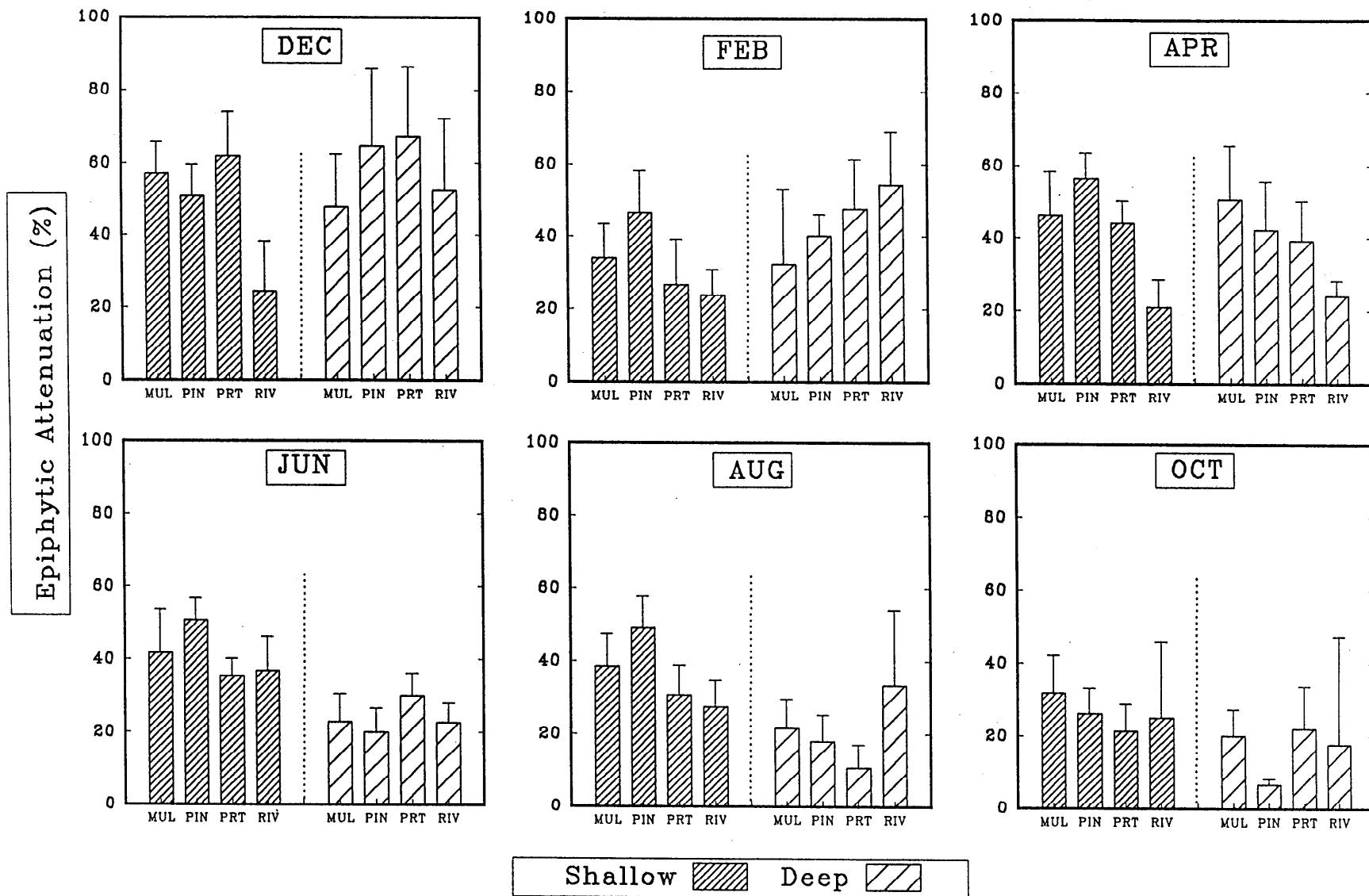


Figure 25. Epiphytic attenuation of PAR by depth, month, and station for Tampa Bay.

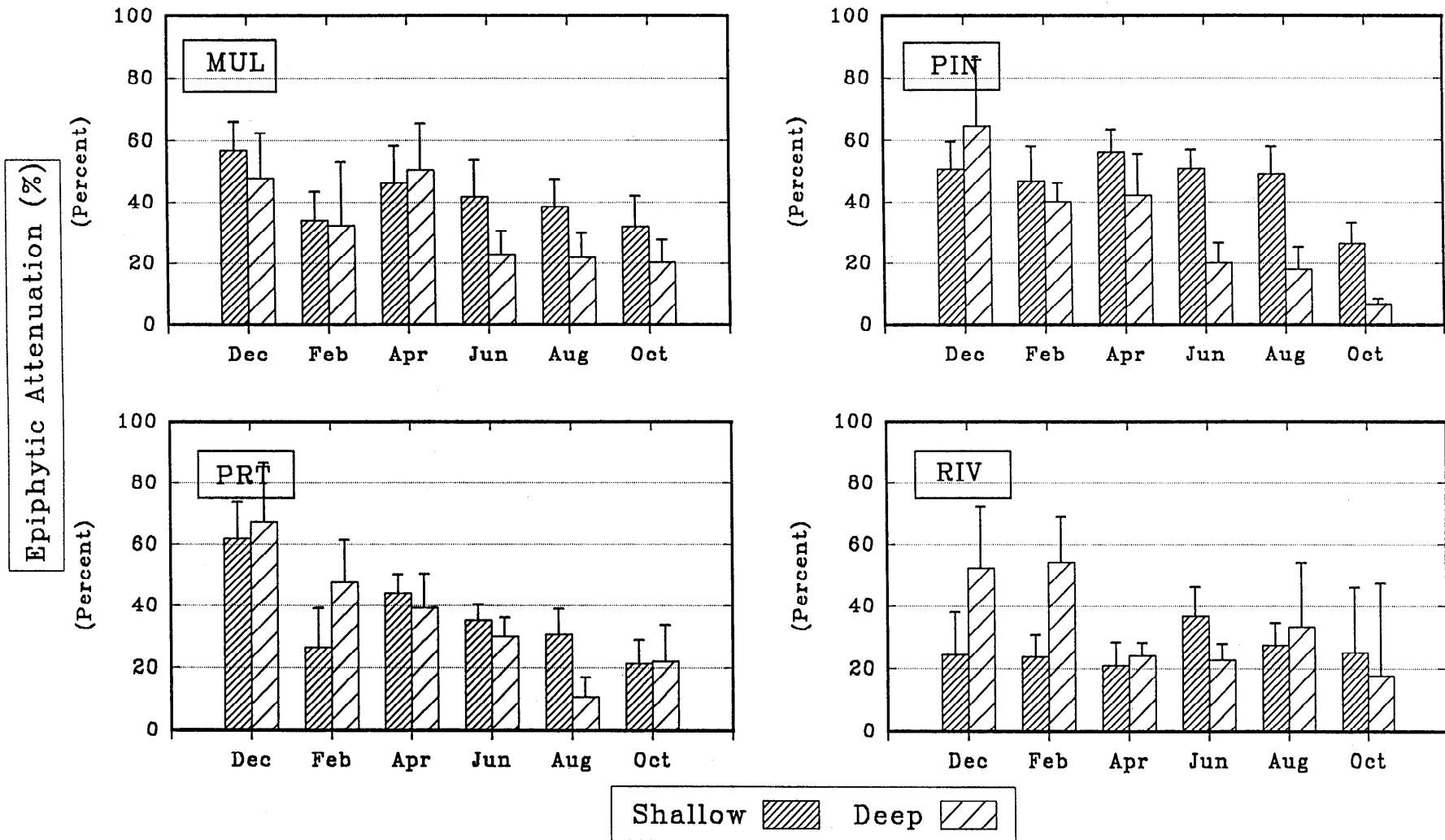


Figure 26, Seasonal patterns of epiphytic attenuation of PAR by station for Tampa Bay.

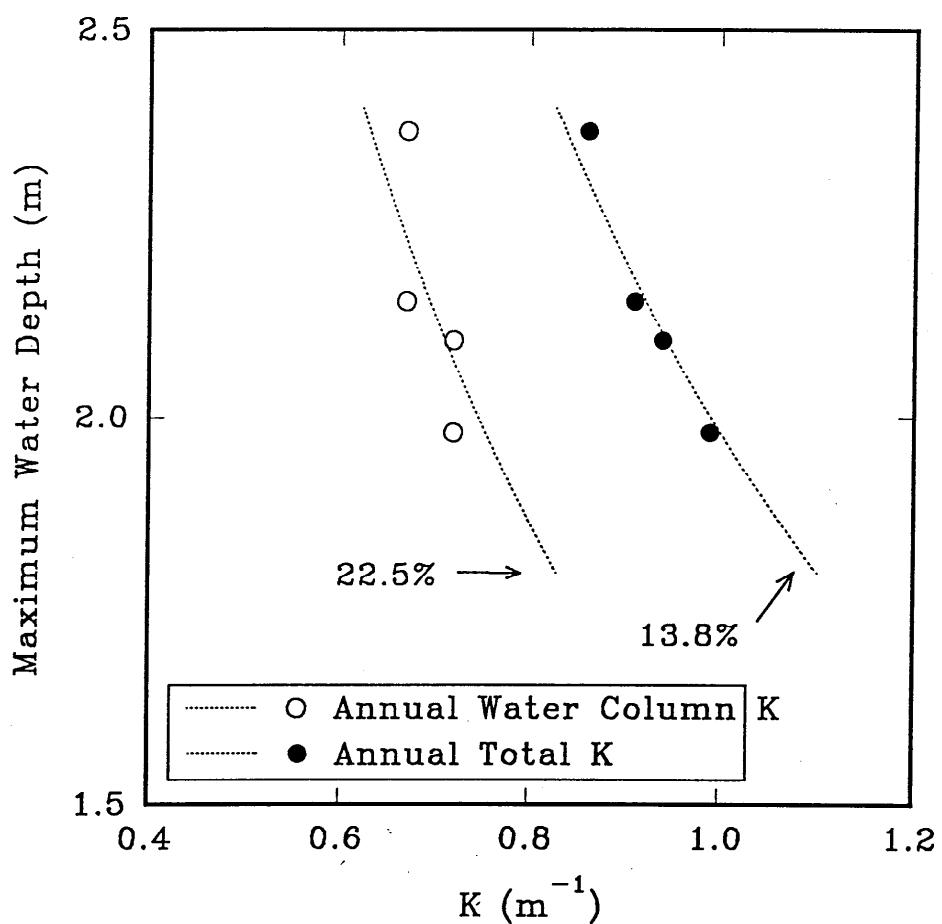


Figure 27. Maximum depth limits of Tampa Bay *Thalassia* stations as a function of attenuation coefficient (K). Attenuation coefficients computed from annual averages of percentage PAR remaining in the water column at depth (annual water column K_0) and with the attenuation due to epiphytes included (annual total K) (see text). Isolumes illustrated are average percentages of four stations.

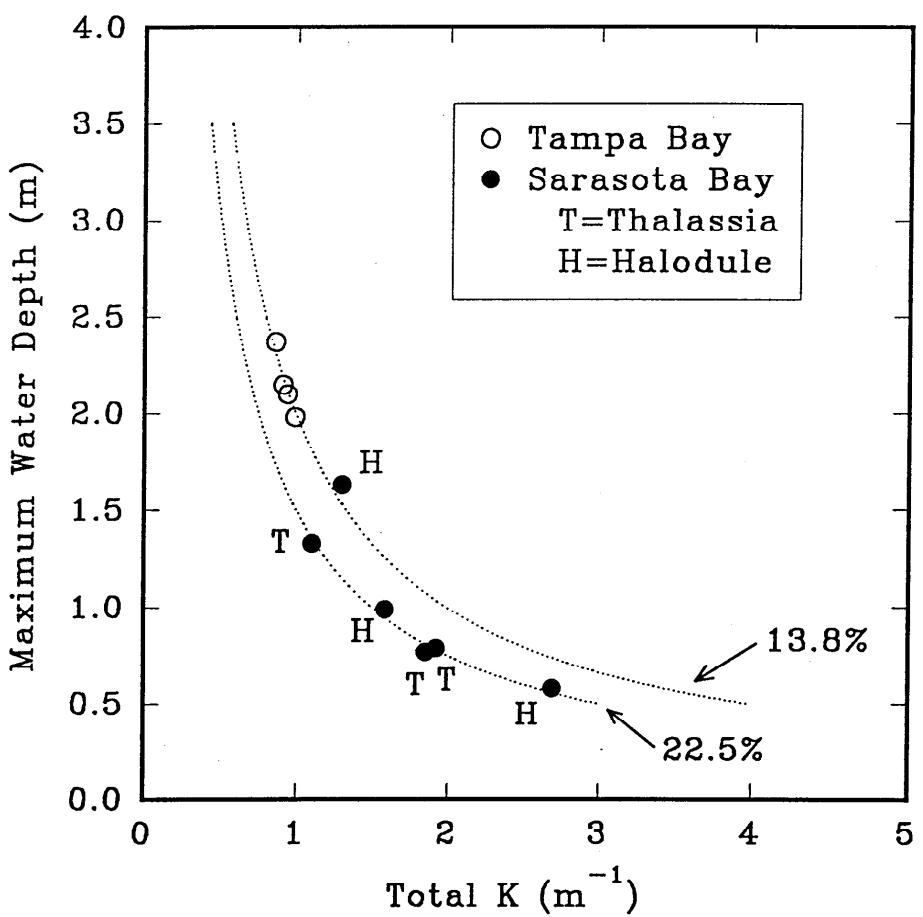


Figure 28. Annual total attenuation coefficients (water column and epiphytic attenuation combined) and maximum depth limits for Tampa and Sarasota Bay stations. Sarasota Bay data produced from biweekly samplings and include measurements at both *Thalassia* and *Halodule* beds.

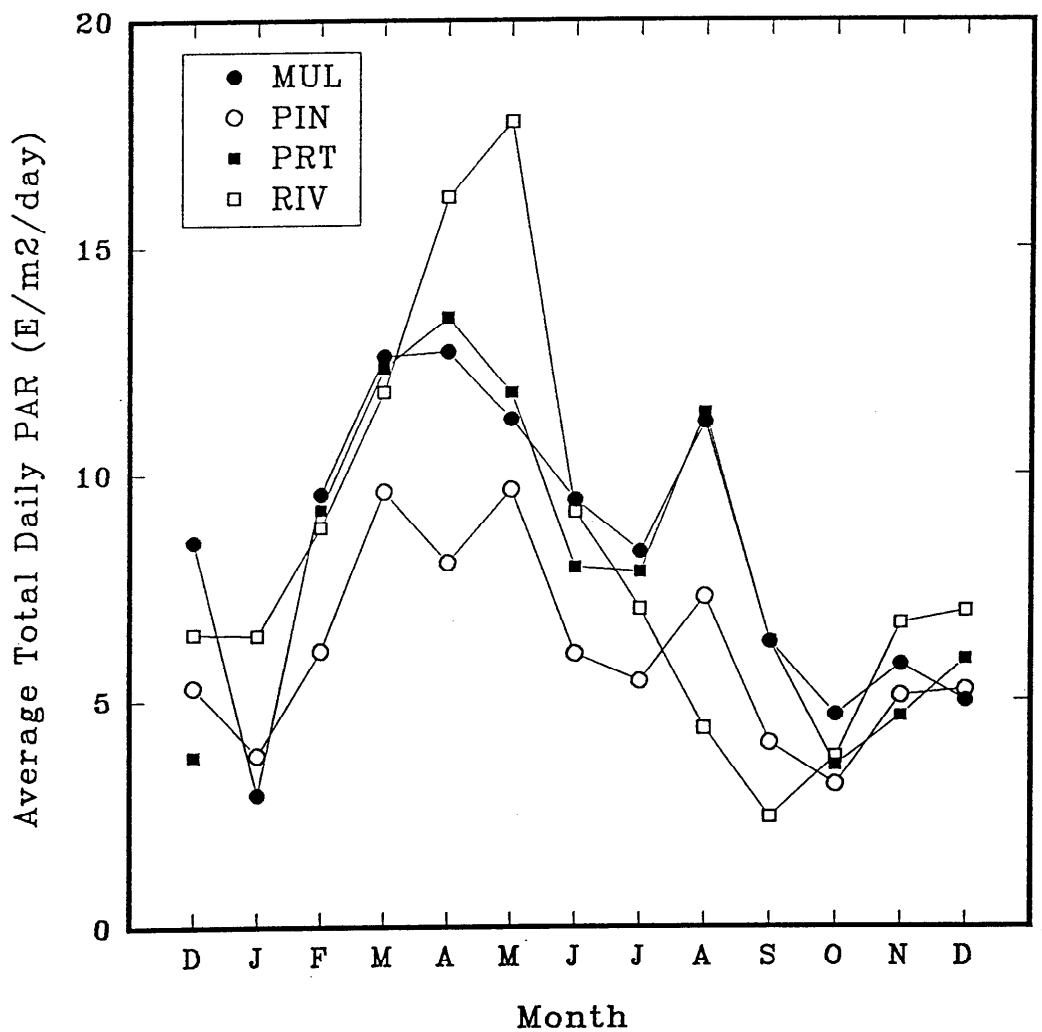


Figure 29. Monthly averages of the total PAR per day received at the maximum depth limits of *Thalassia* beds in Tampa Bay.

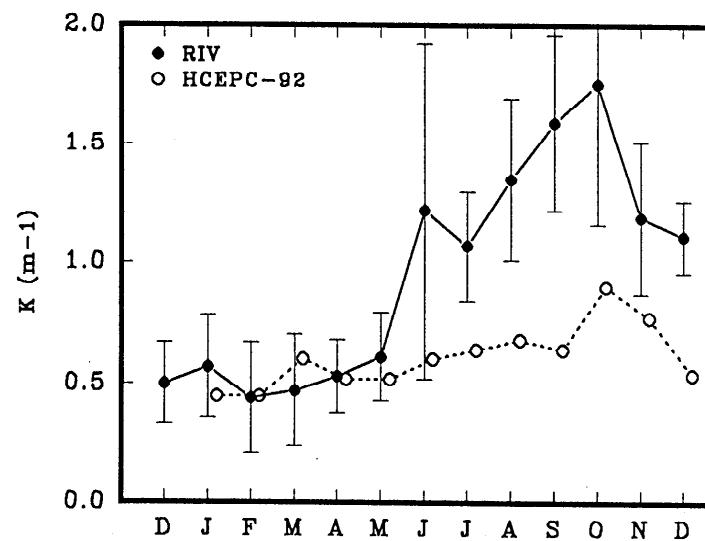
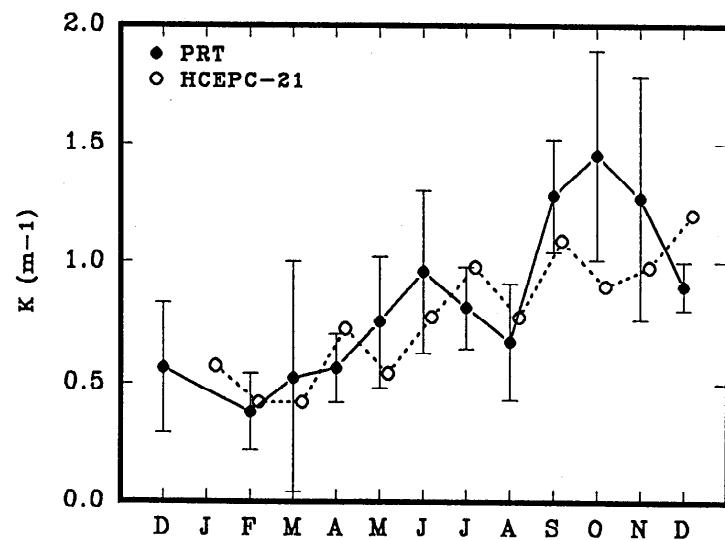
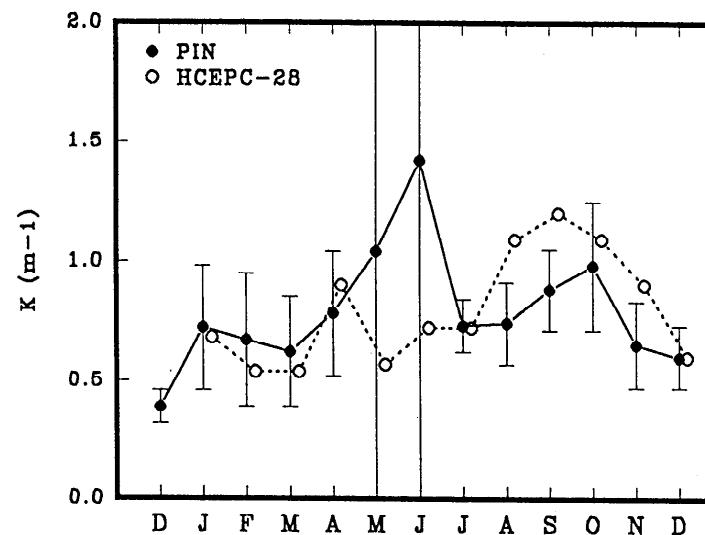
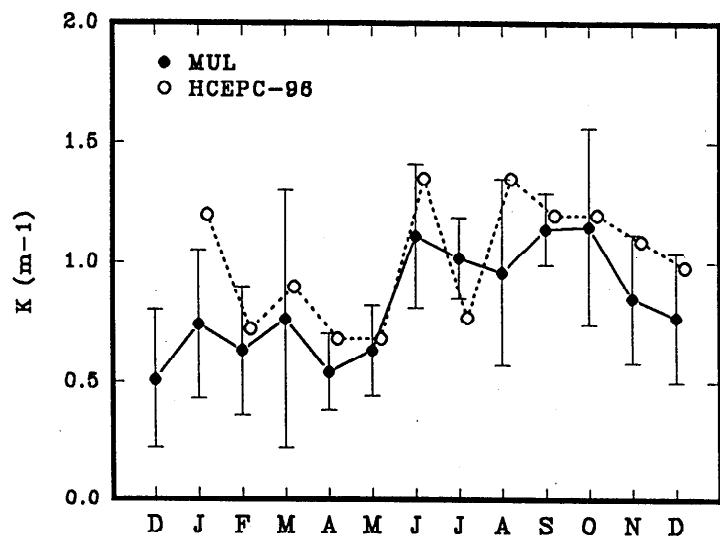


Figure 30. Comparison of monthly mean attenuation coefficients (1000-1400 hours) determined from continuous monitors and measured during monthly interval samplings by Hillsborough County Environmental Protection Commission. Stations compared are the closest available to continuous light sites, although for the RIV site, the nearest HCEPC is some distance away.

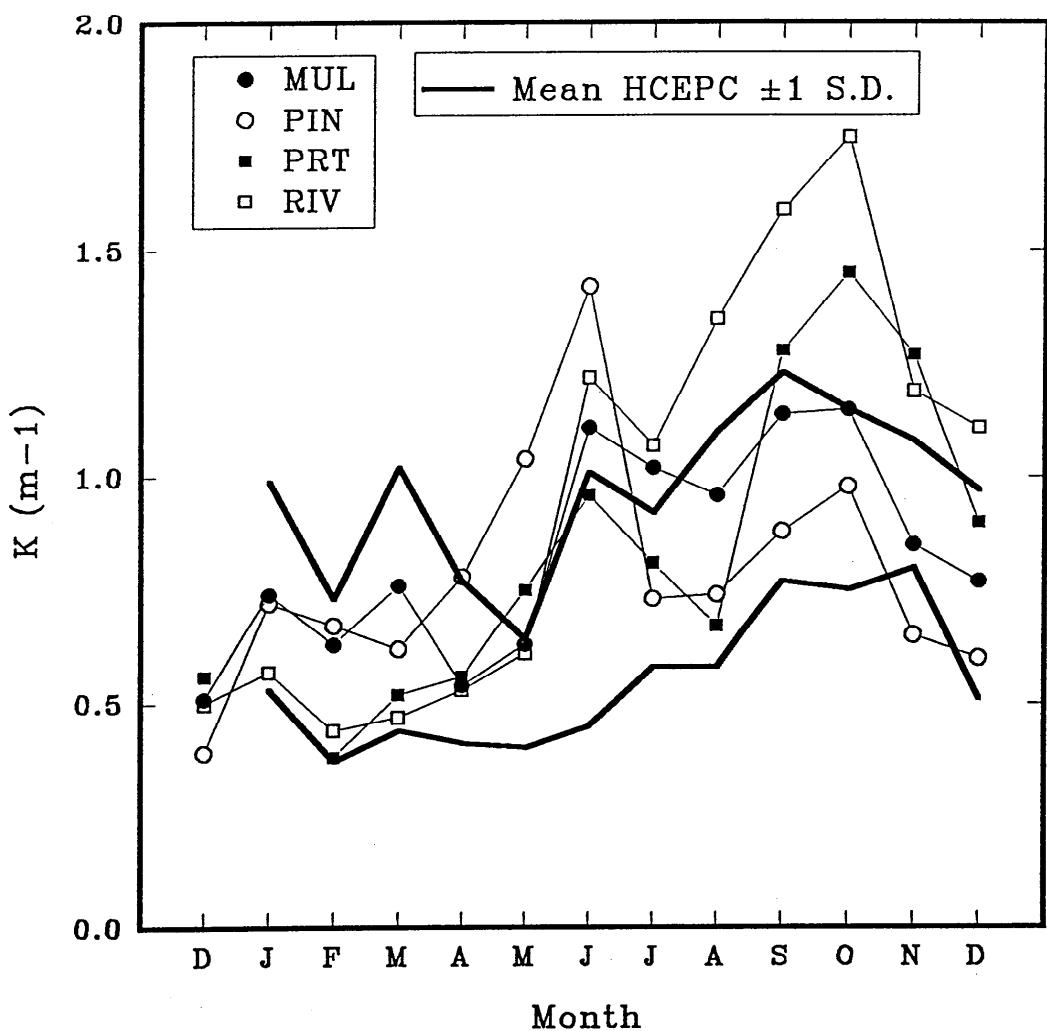


Figure 31. Comparison of monthly mean attenuation coefficients determined by continuous monitoring with the envelope described by the HCEPC stations in lower Middle and Lower Tampa Bay (HCEPC Stations 19, 21, 23, 24, 25, 28, 90, 91, 92, 95 and 96).

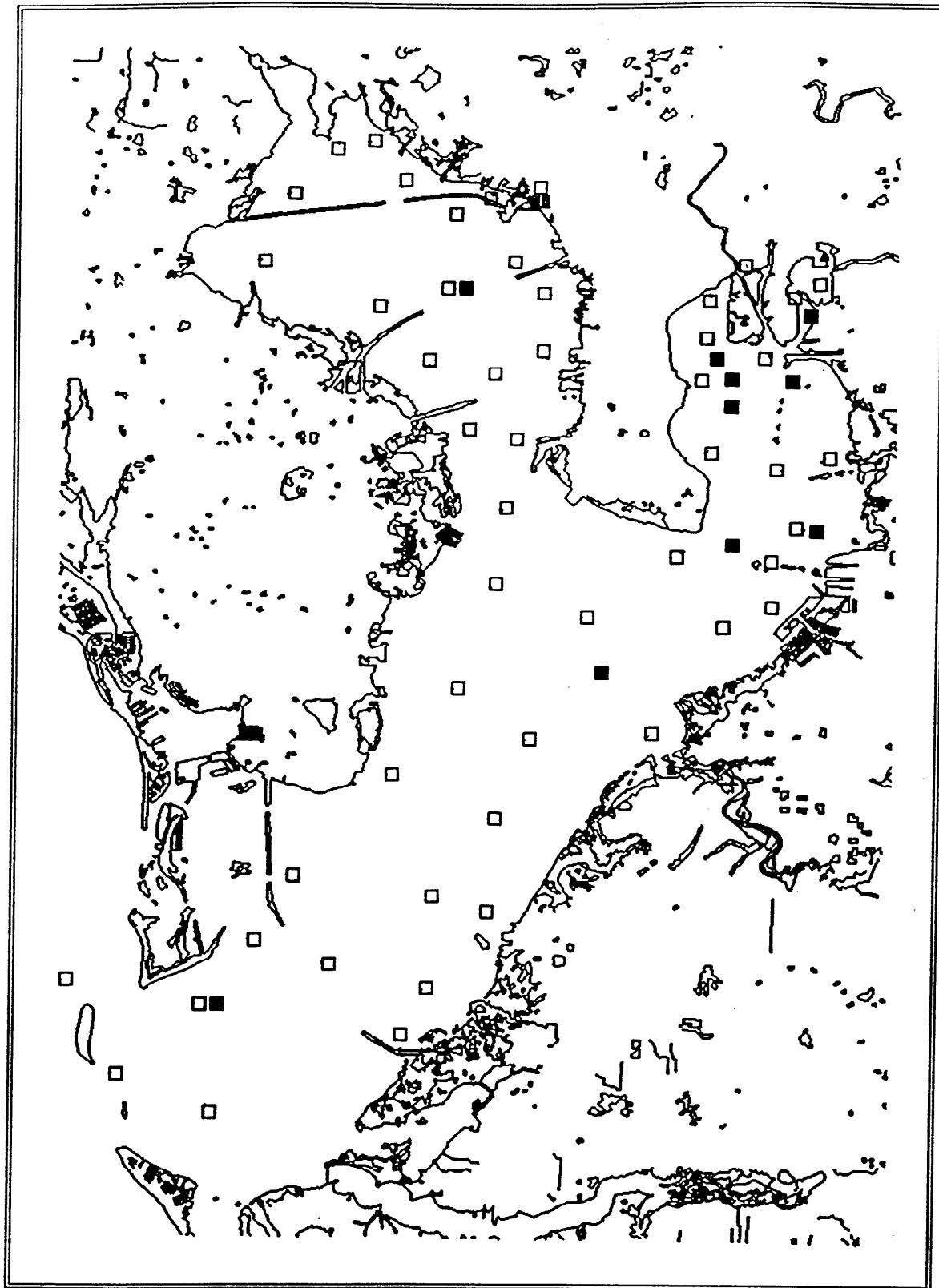
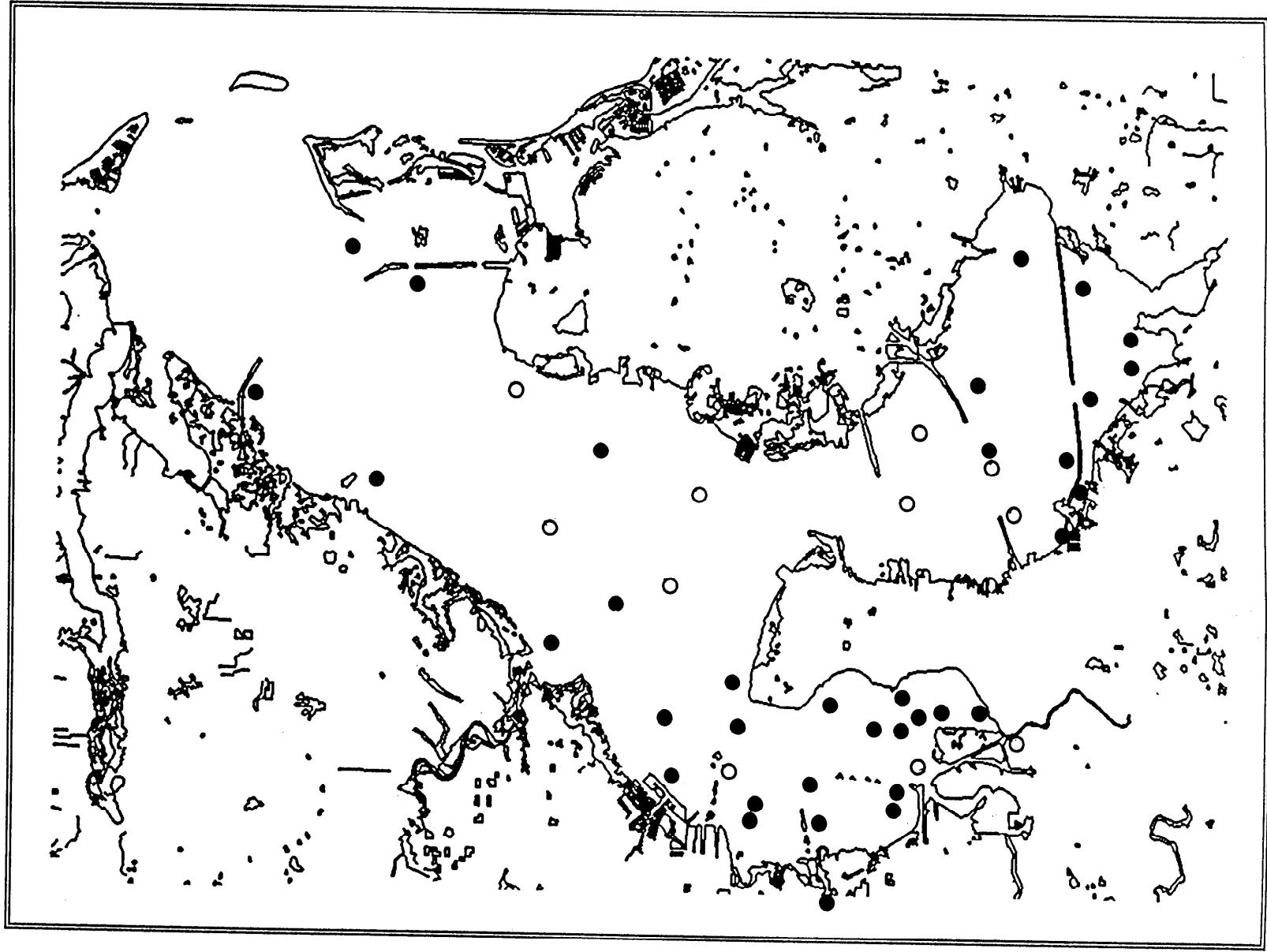


Figure 32. Locations of Hillsborough County (□) and City of Tampa (■) routine water quality monitoring stations.



Figure 33. Routine monitoring stations. Stations (○) which meet annual average water clarity requirements for *Thalassia* under moderate (38.7 %) epiphytic attenuation, but not under high (50.0%) attenuation. Stations (●) which do not meet requirements under moderate or high epiphytic attenuation.

Figure 34. Routine monitoring stations. Stations (○) which meet growing season (May-Sept) average water clarity requirements for *Thalassia* under moderate (38.7%) epiphytic attenuation, but not under high (50.0%) attenuation. Stations (●) which do not meet requirements under moderate or high epiphytic attenuation.



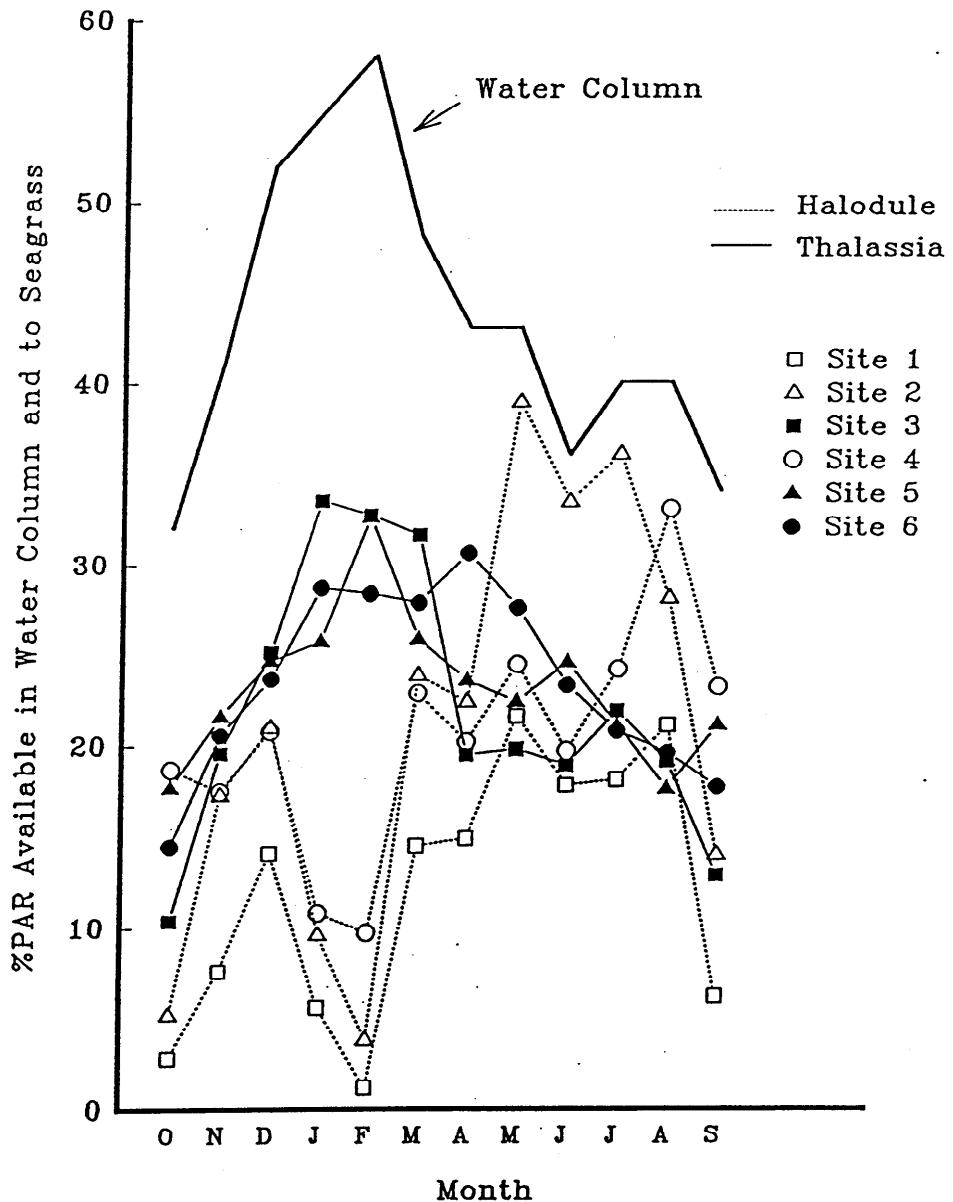


Figure 35. Seasonal patterns of total attenuation (both from water column and epiphytic load) on *Thalassia* and *Halodule* from Sarasota Bay. Samples collected from the maximum depth limits of individual stations and under a variety of nutrient loading conditions (Source: Dixon and Kirkpatrick, 1995).

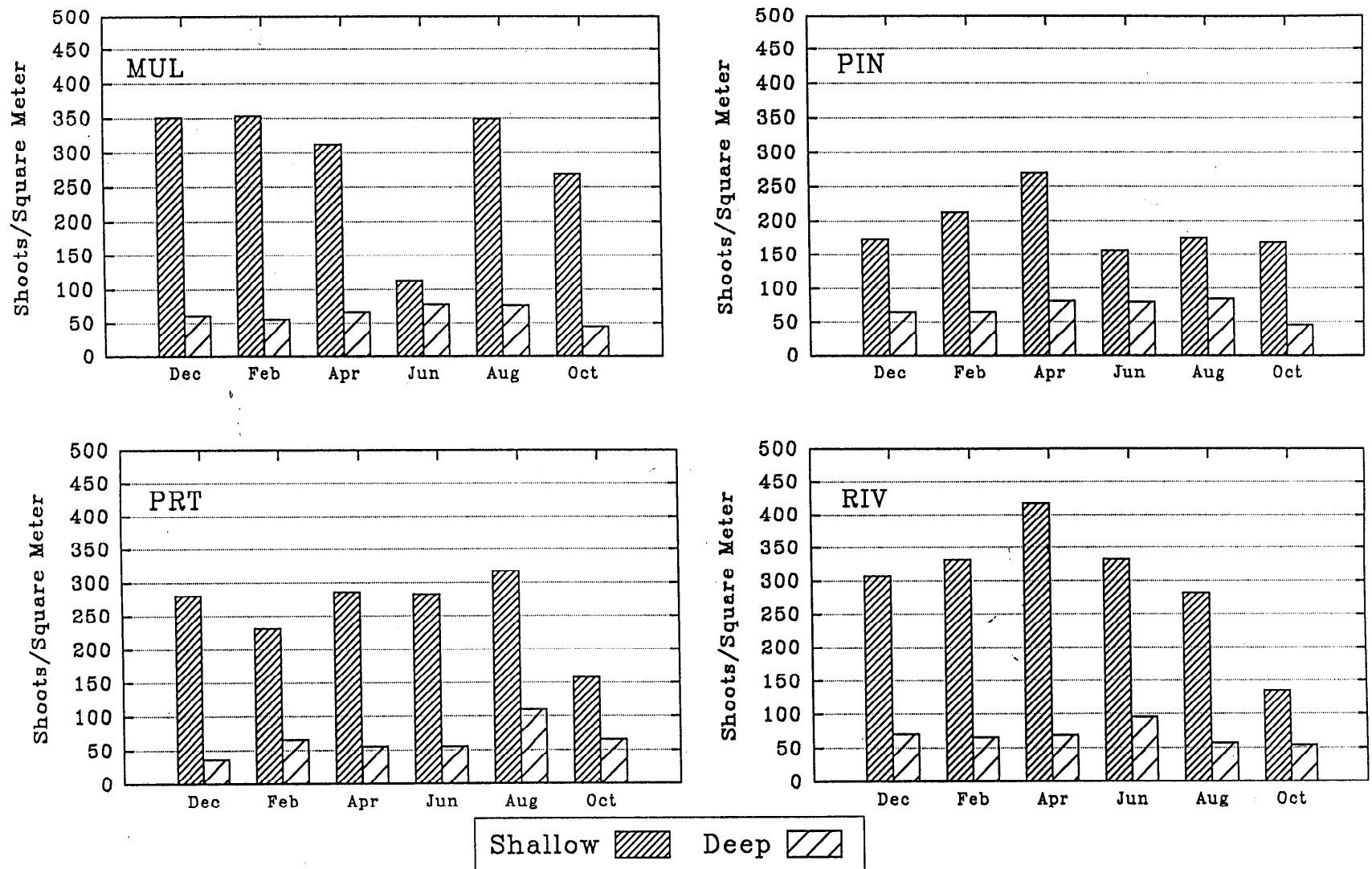


Figure 36. *Thalassia* shoot density (shoots m^{-2}) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means of approximately 40 quadrat counts.

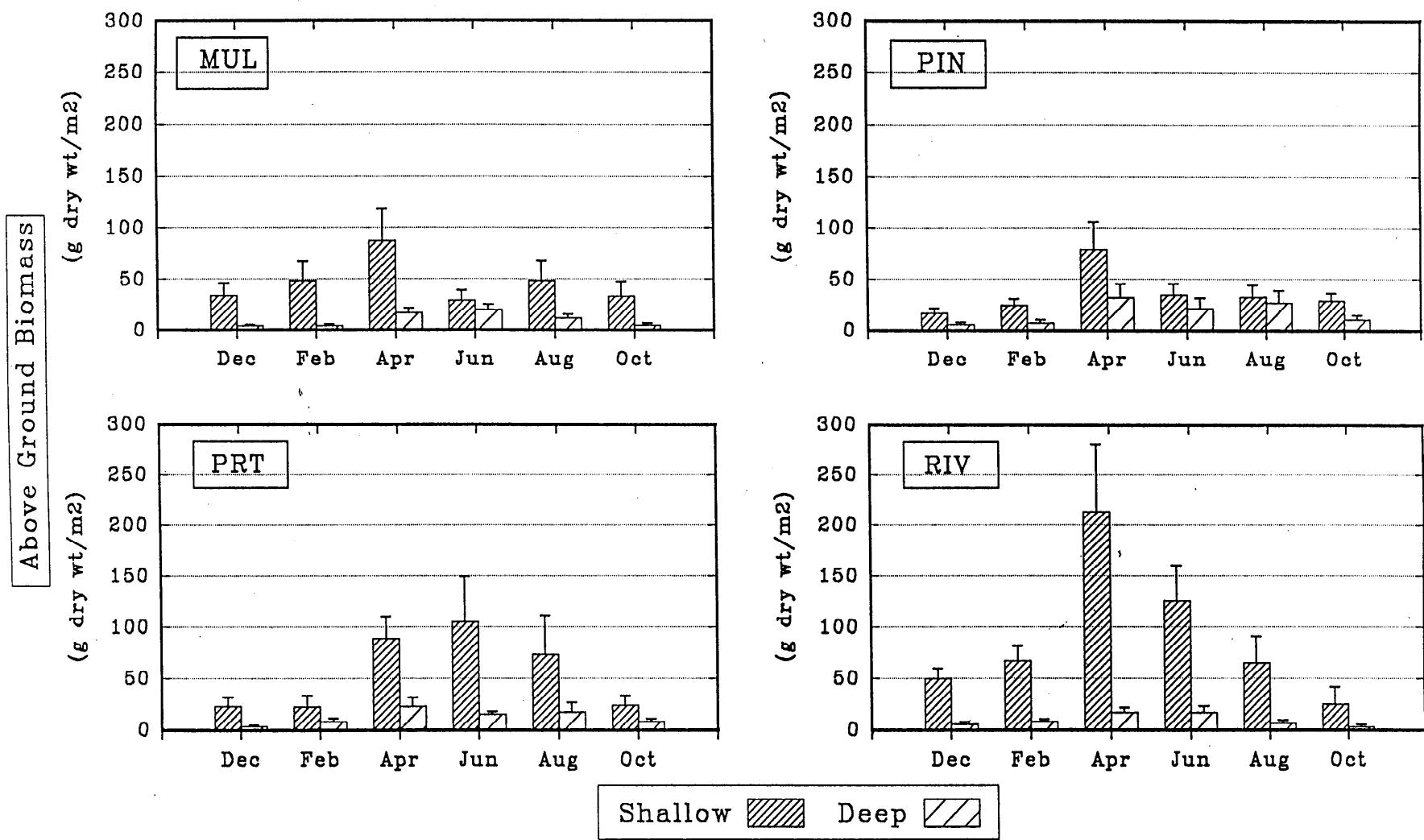


Figure 37. *Thalassia* above-ground biomass (gdwt m^{-2}) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 10$.

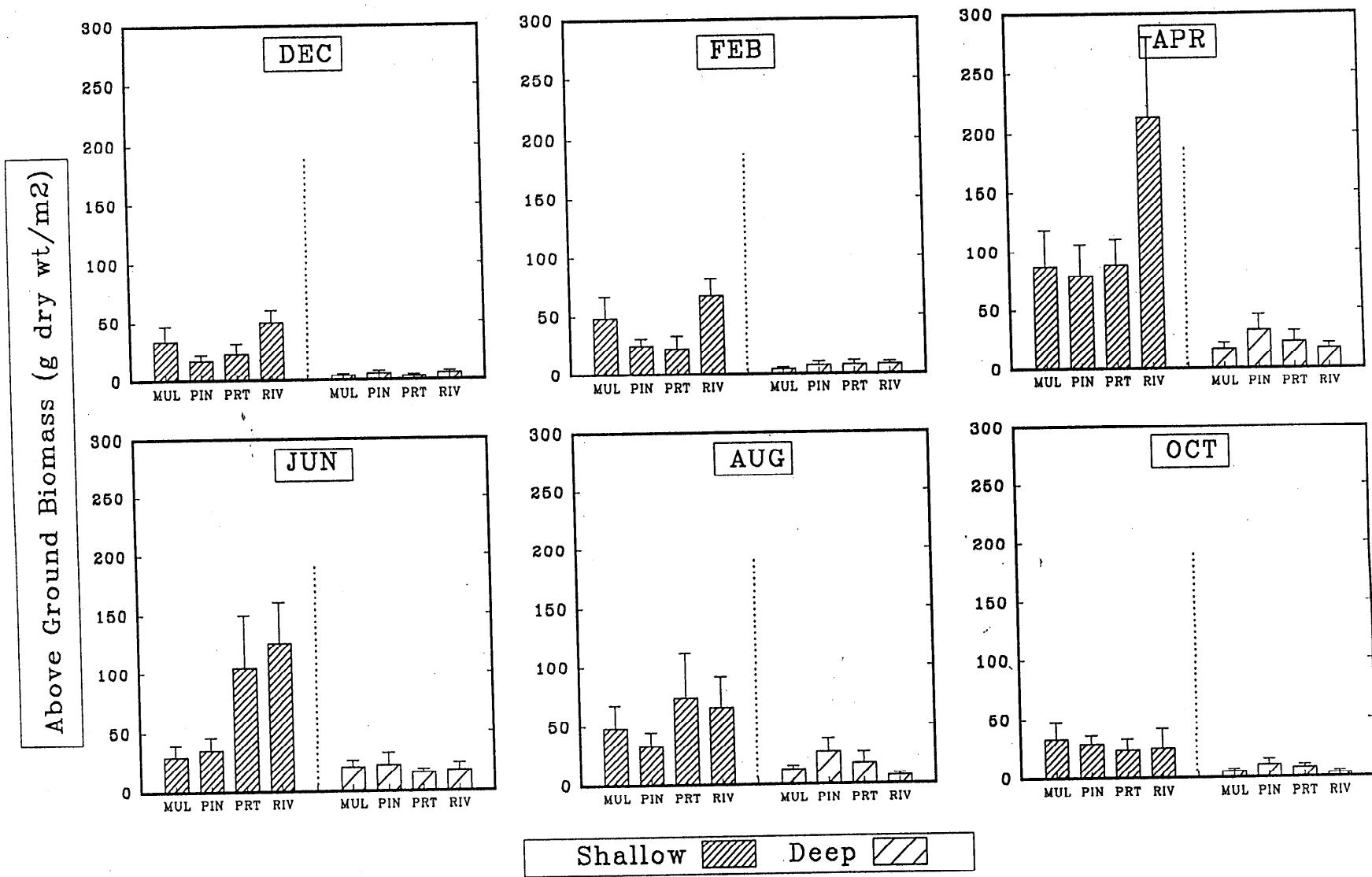


Figure 38. *Thalassia* above-ground biomass (gdwt m⁻²). Comparisons among shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10).

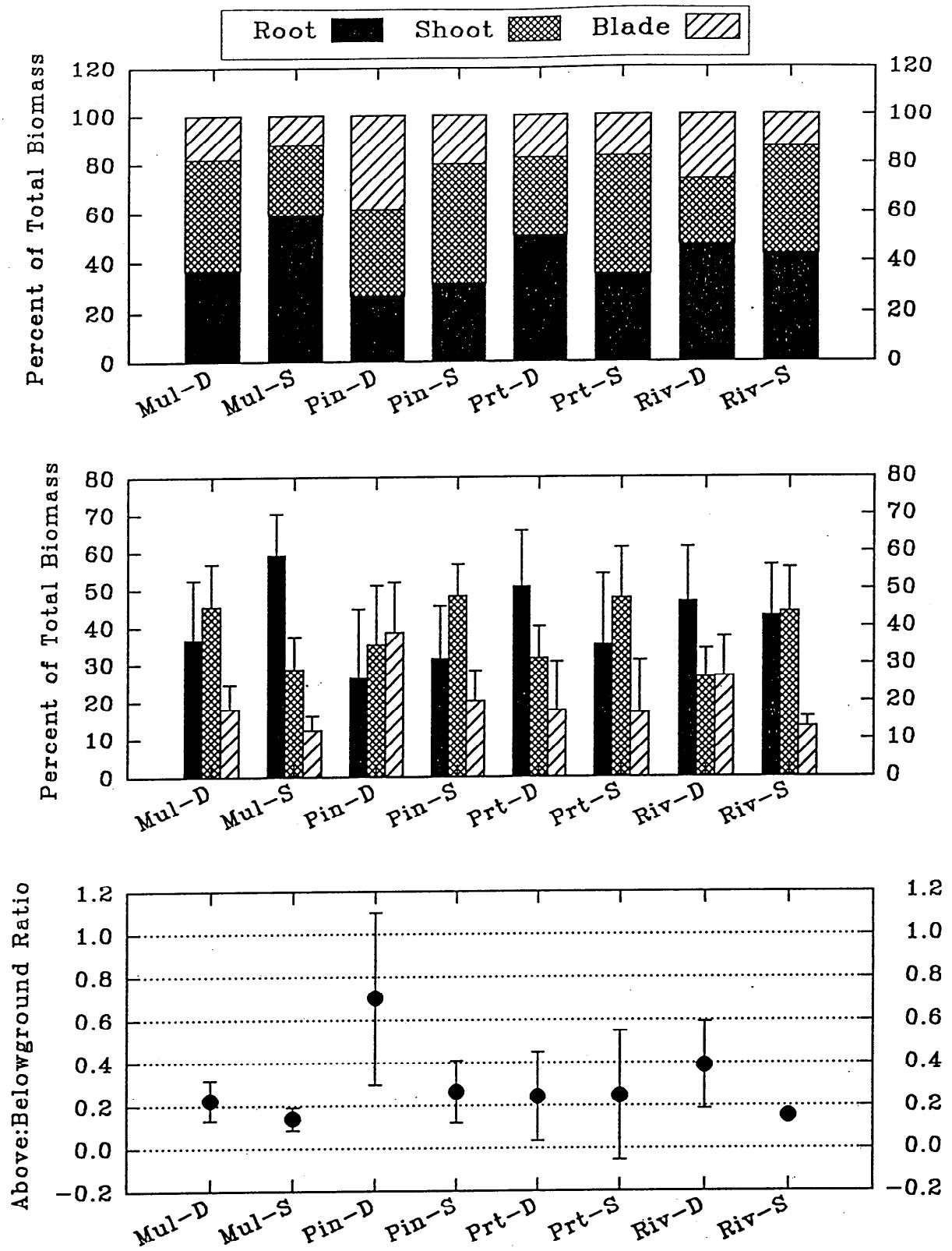


Figure 39. Percent of total *Thalassia* biomass from roots and rhizomes, short shoots, and blades at all stations during December 1994. Ratio of above to below-ground biomass. Values are means \pm s.d.; n = 10.

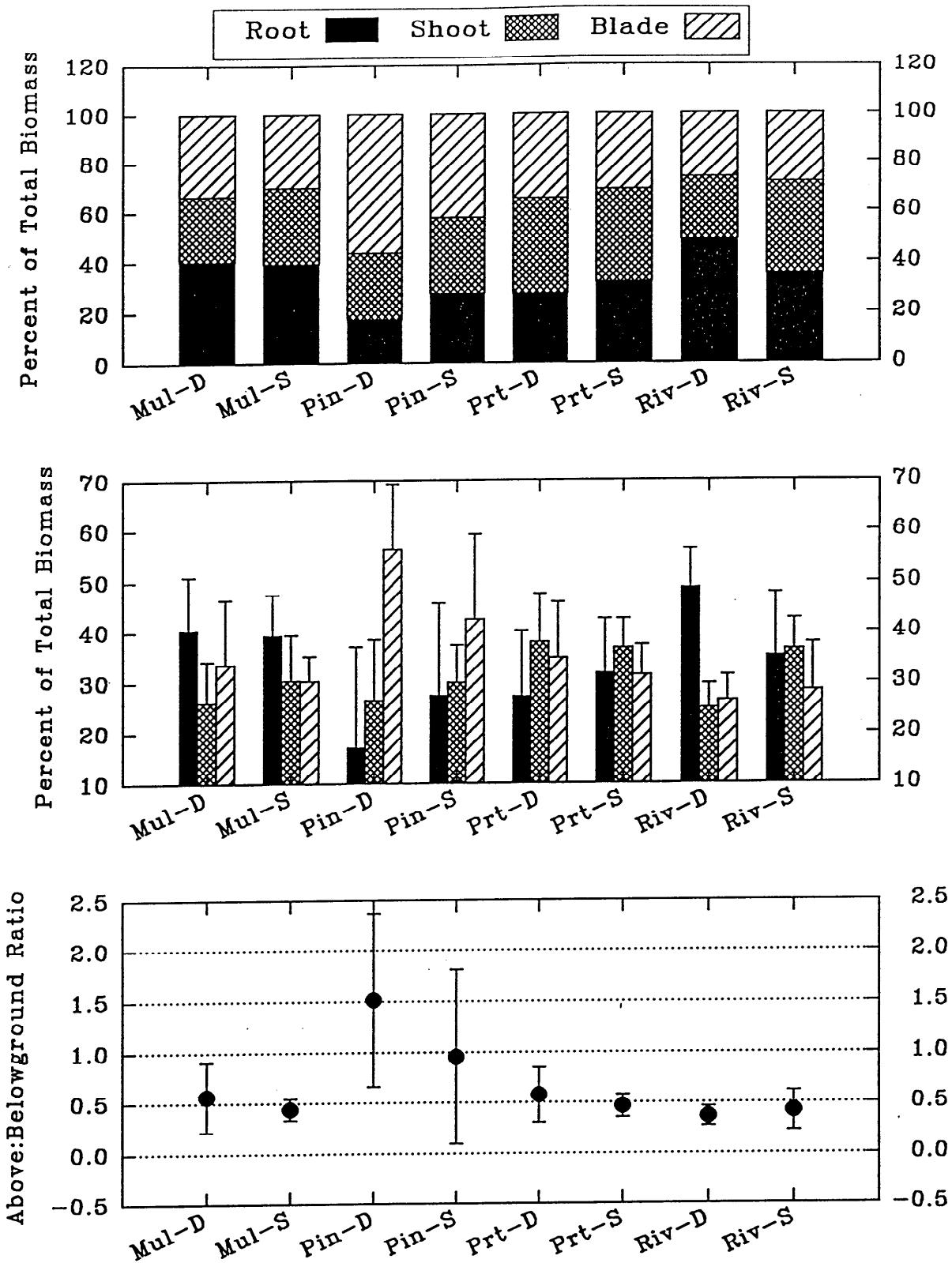


Figure 40. Percent of total *Thalassia* biomass from roots and rhizomes, short shoots, and blades at all stations during April 1994. Ratio of above to below-ground biomass. Values are means ± 1 s.d.; n = 10.

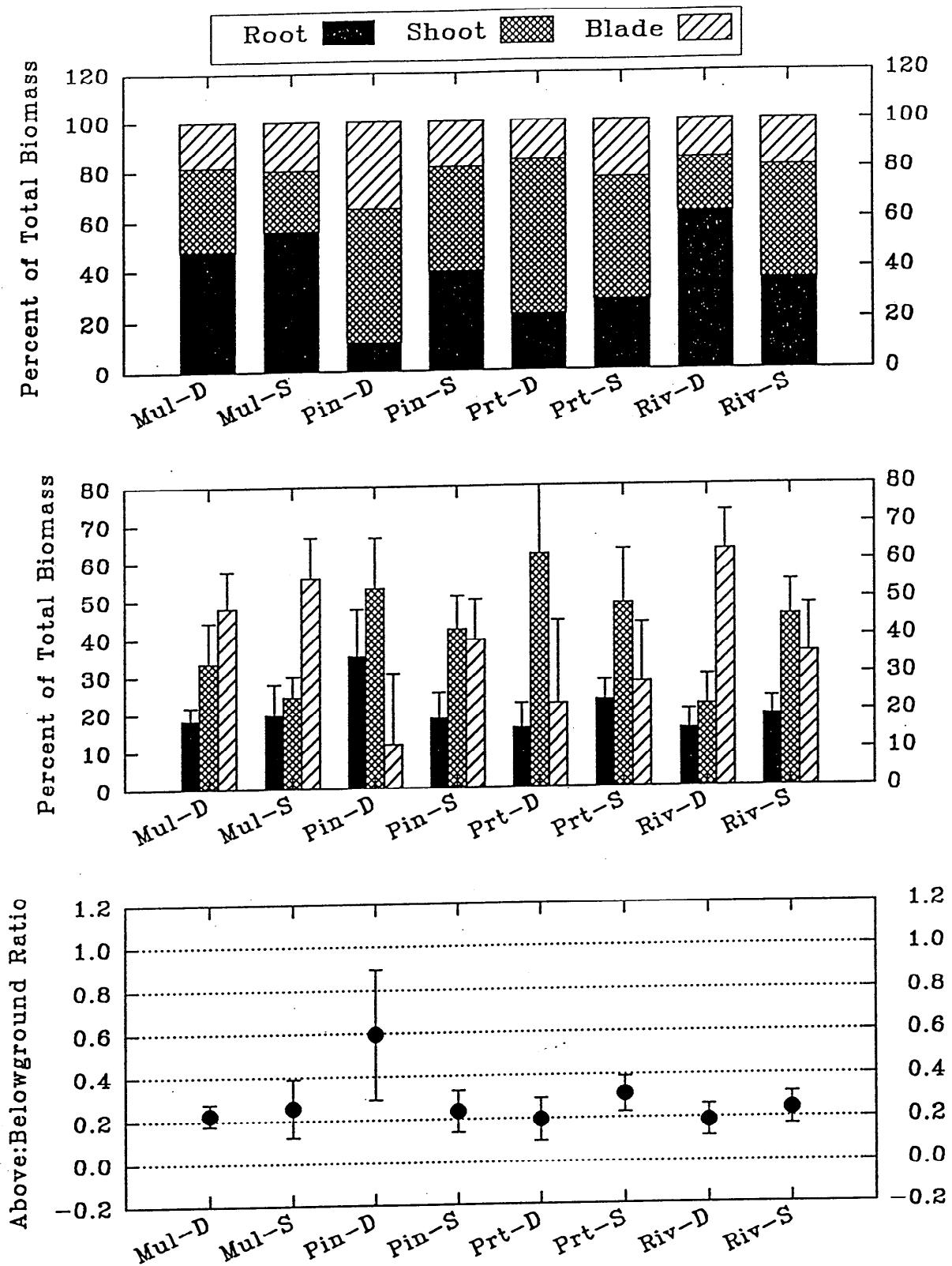


Figure 41. Percent of total *Thalassia* biomass from roots and rhizomes, short shoots, and blades at all stations during August 1994. Ratio of above to below-ground biomass. Values are means ± 1 s.d.; n = 10.

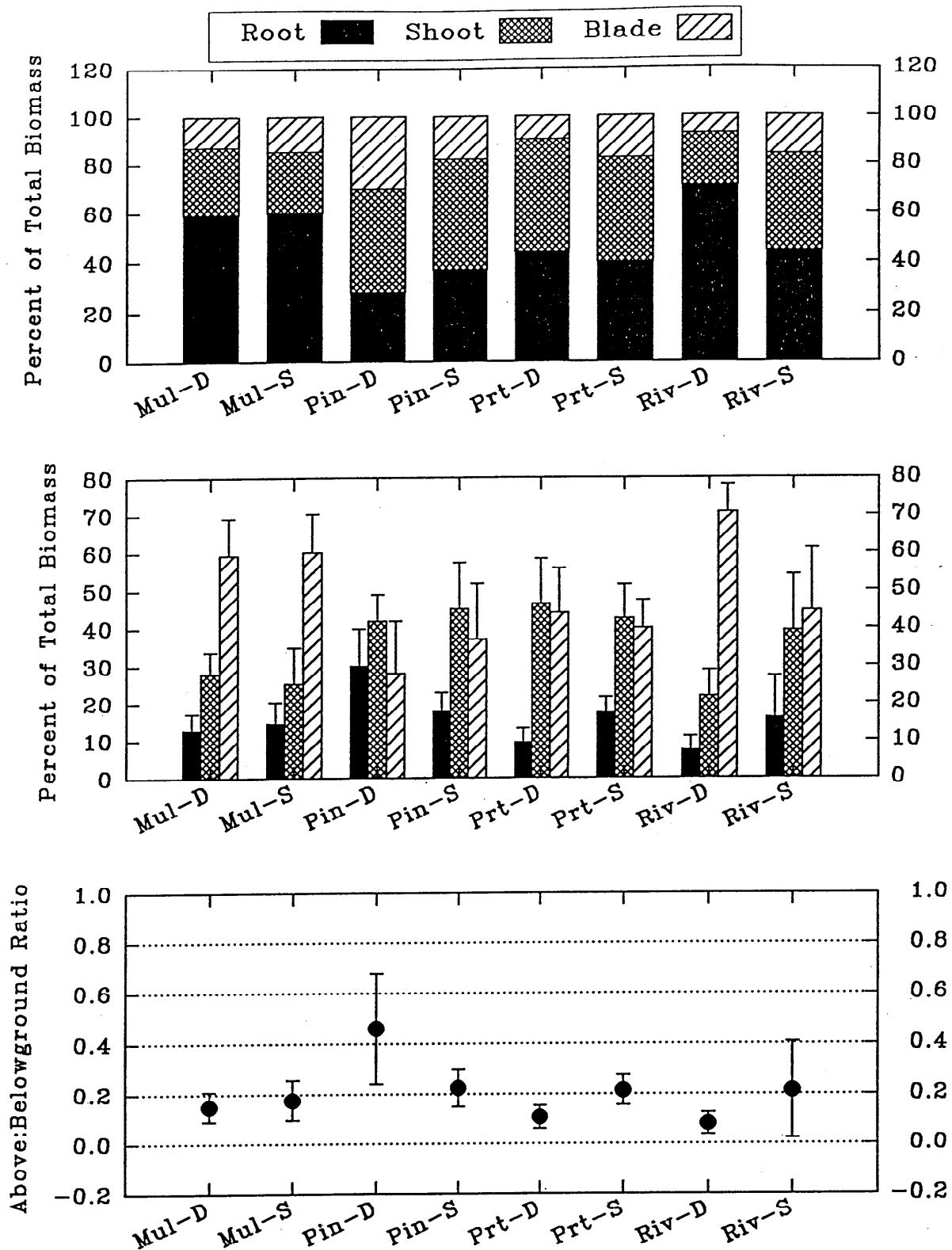


Figure 42. Percent of total *Thalassia* biomass from roots and rhizomes, short shoots, and blades at all stations during October 1994. Ratio of above to below-ground biomass. Values are means ± 1 s.d.; n = 10.

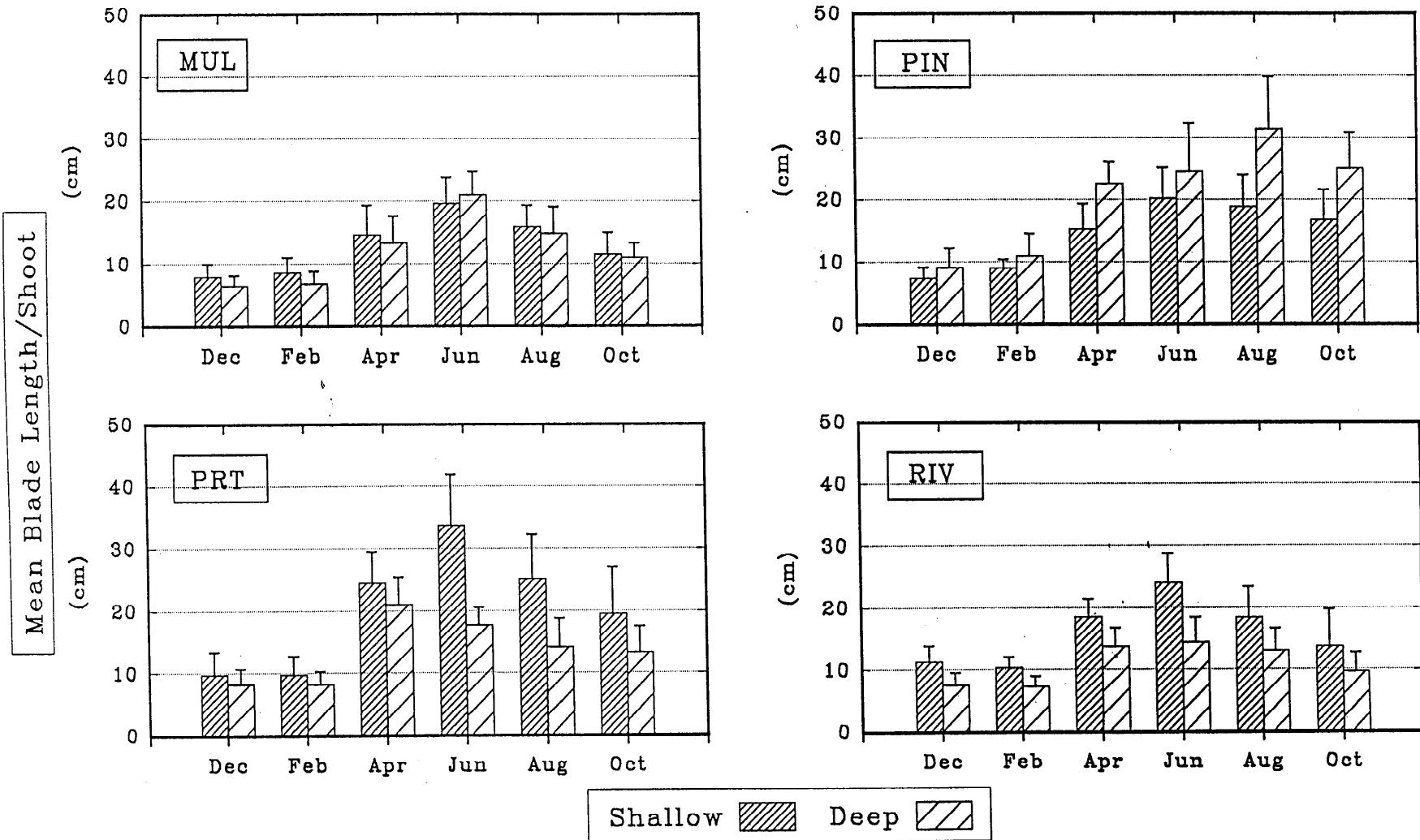


Figure 43. Mean *Thalassia* blade length (cm shoot^{-1}) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

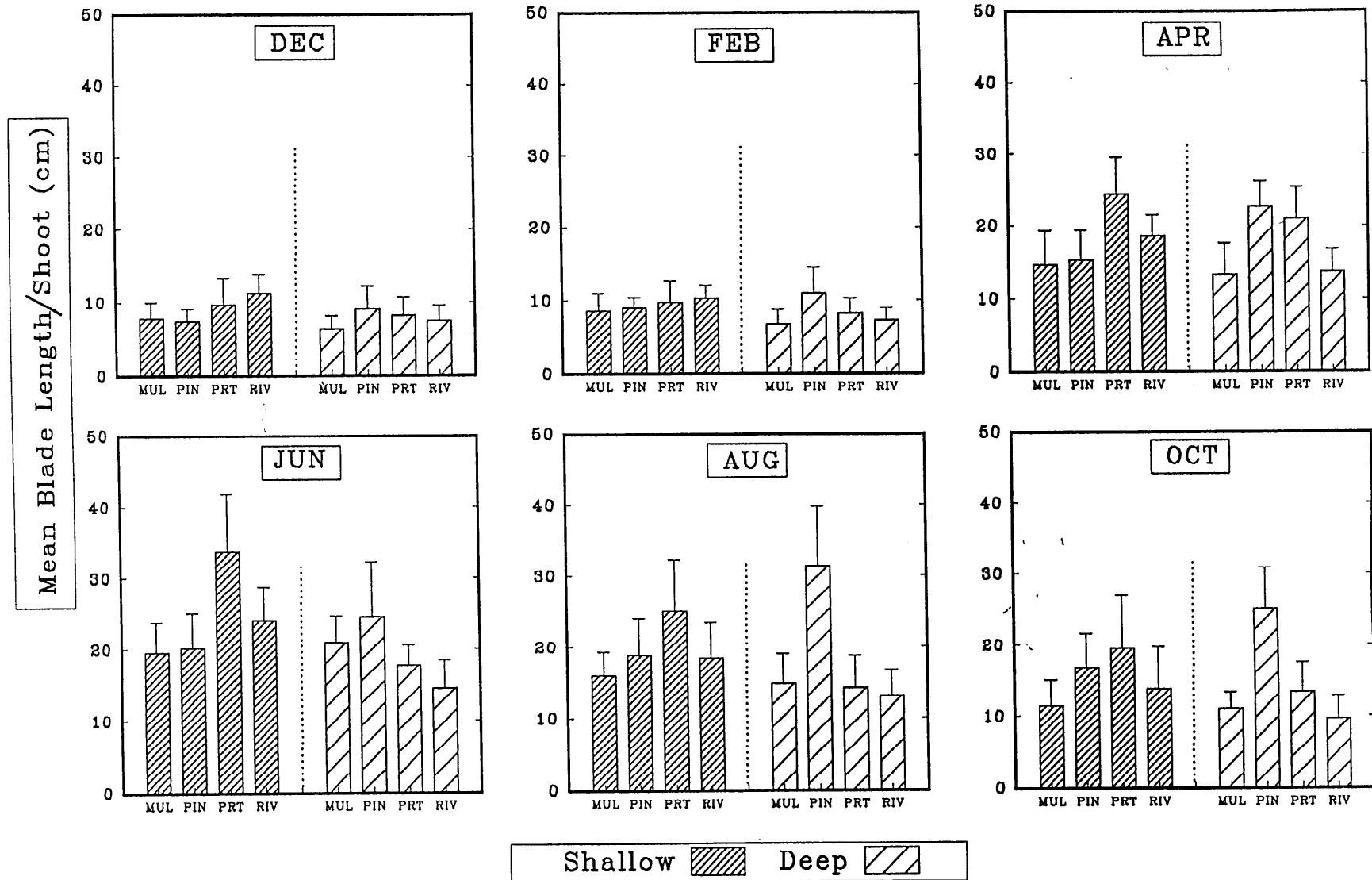


Figure 44. Mean *Thalassia* blade length (cm shoot⁻¹). Comparison among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 15.

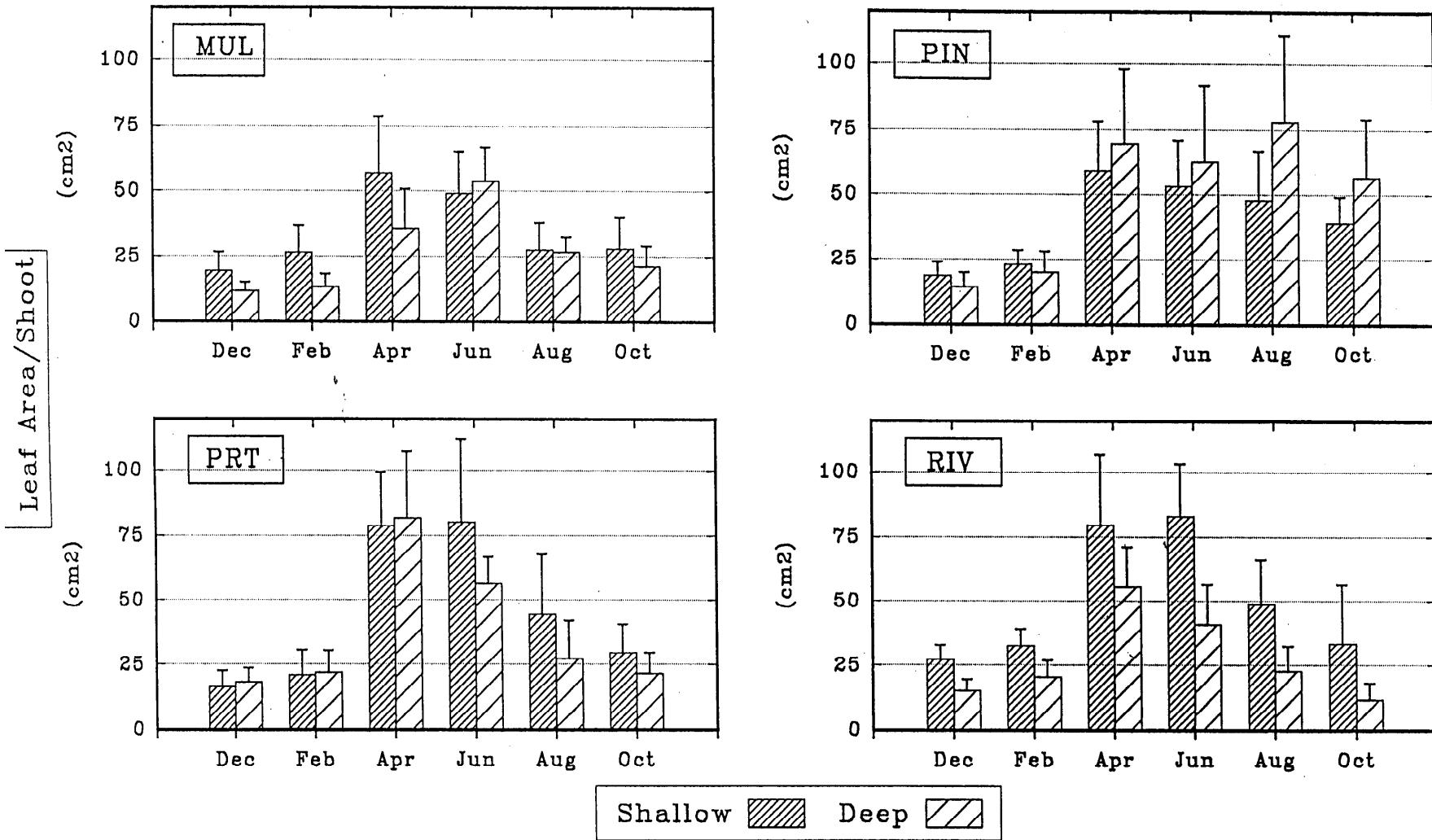


Figure 45. *Thalassia* leaf area ($\text{cm}^2 \text{ shoot}^{-1}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

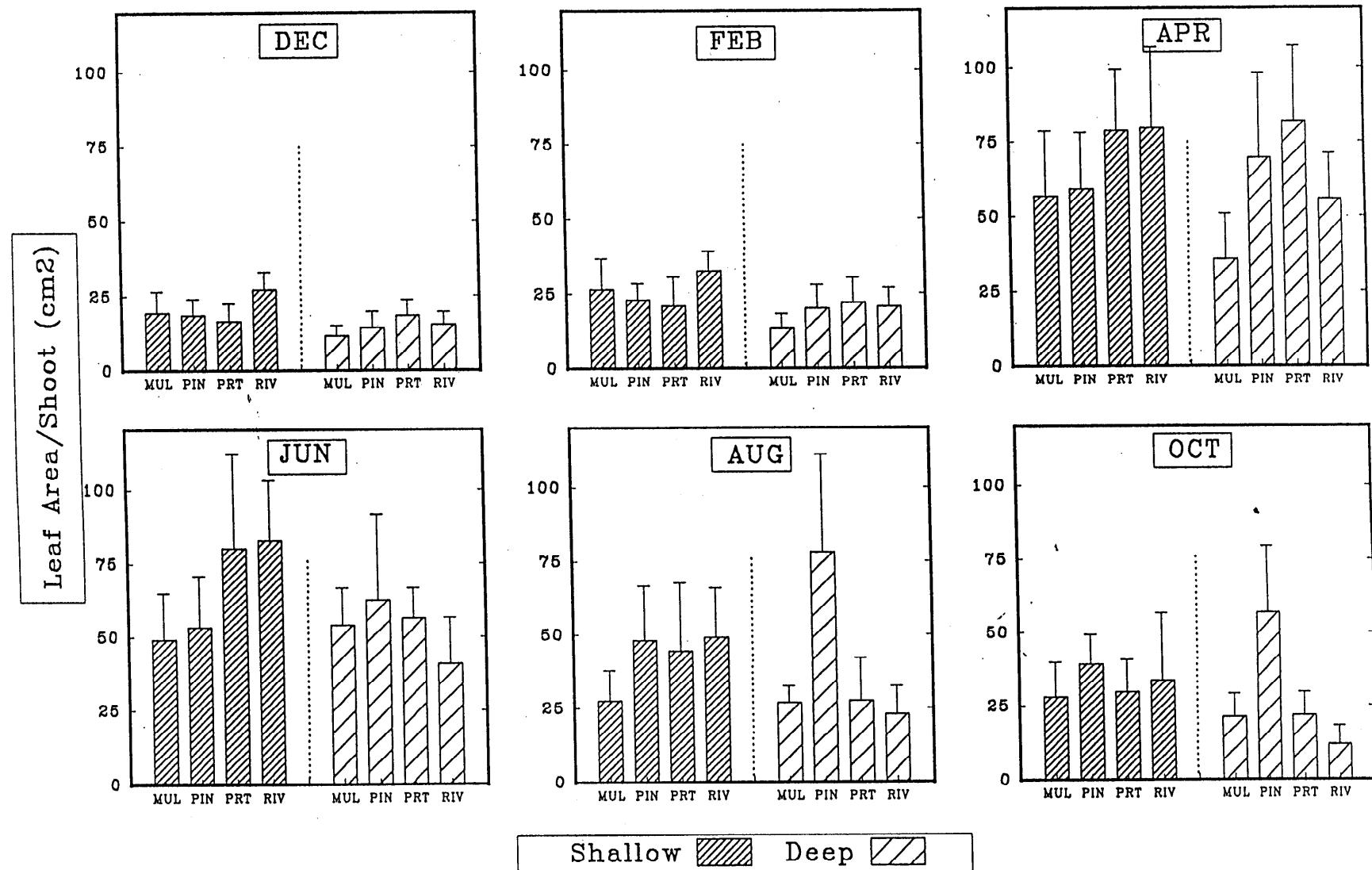


Figure 46. *Thalassia* leaf area ($\text{cm}^2 \text{ shoot}^{-1}$). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

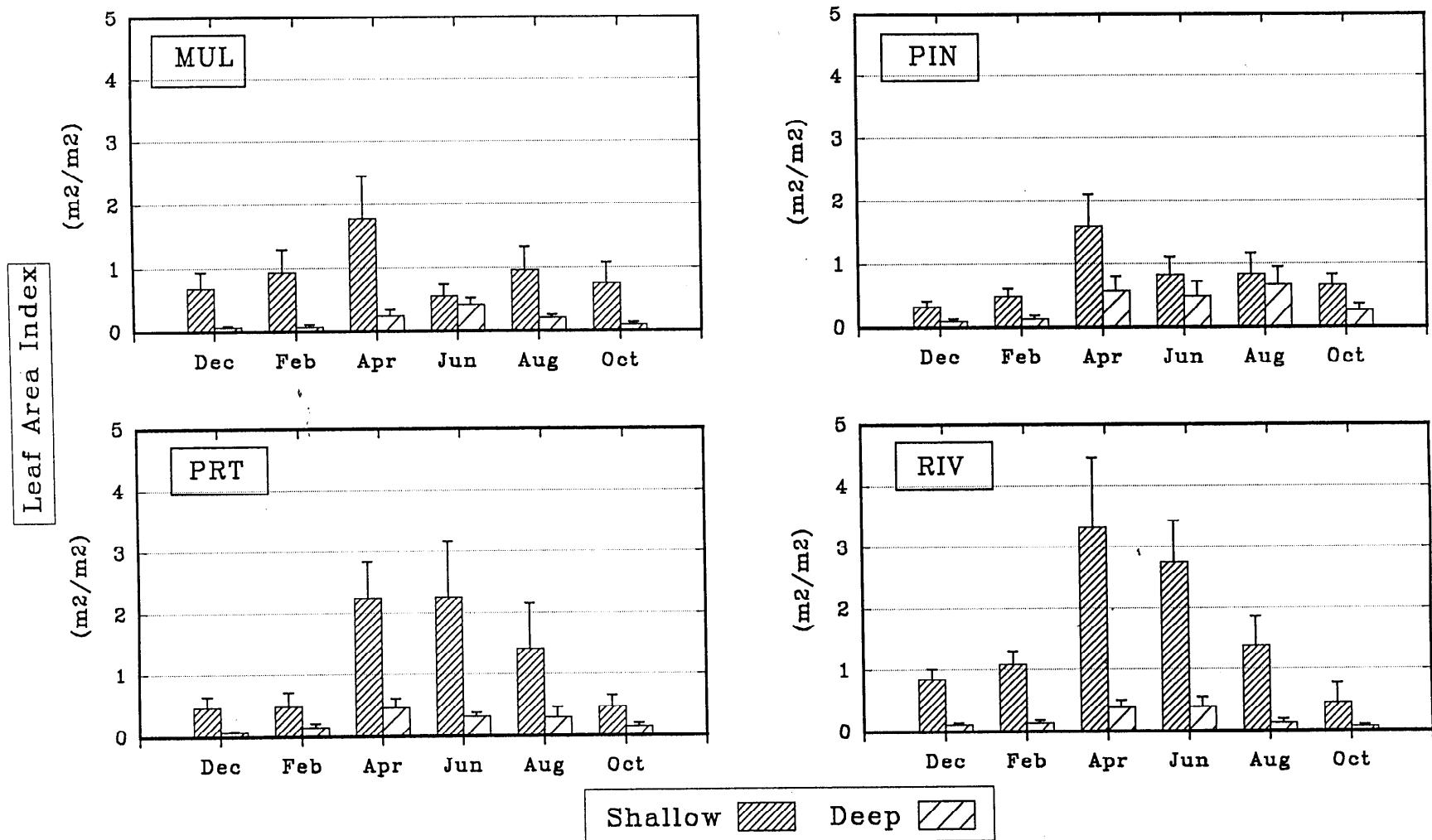


Figure 47. ***Thalassia*** leaf area index ($\text{m}^2 \text{ m}^{-2}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

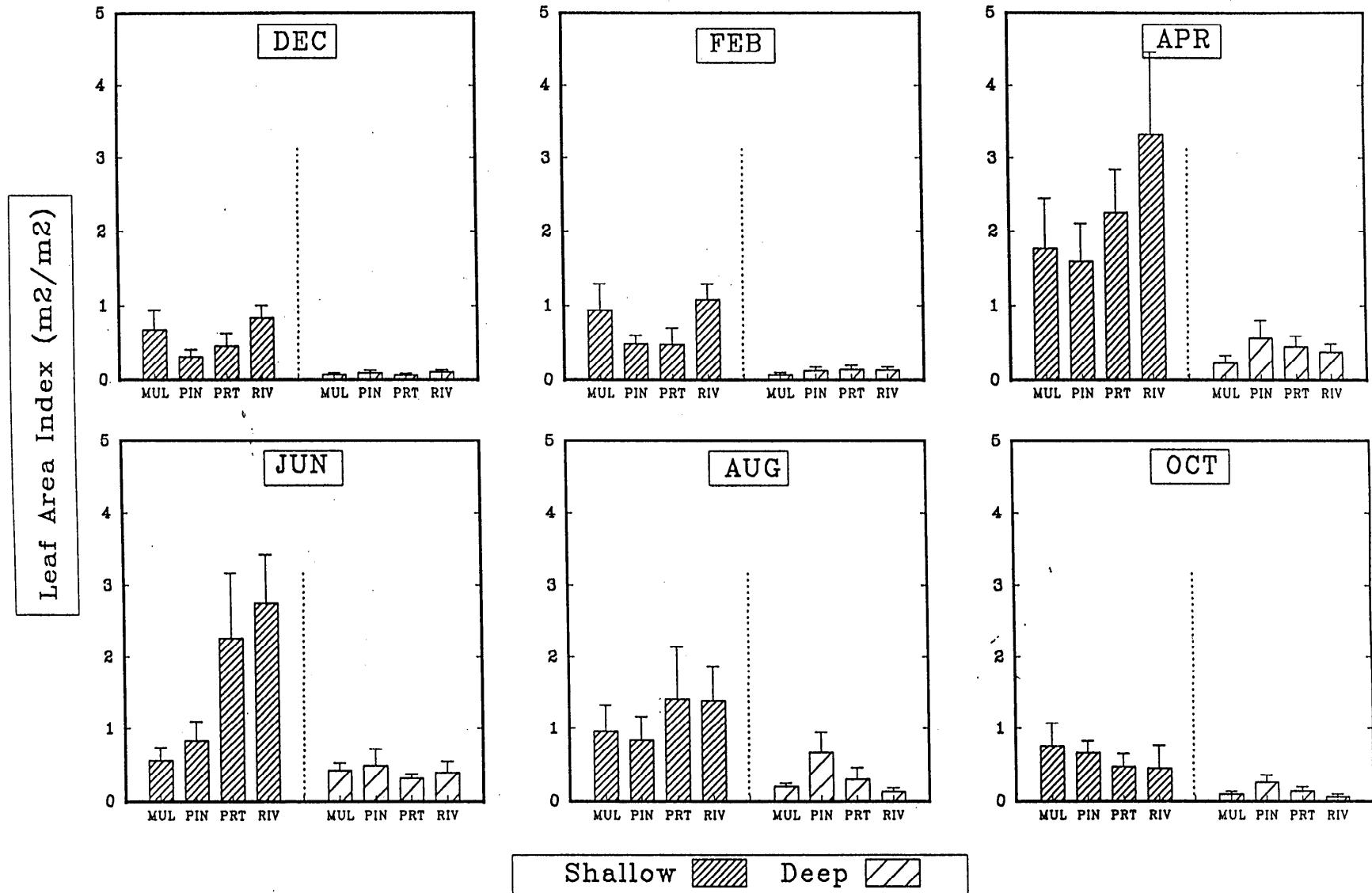


Figure 48. ***Thalassia*** leaf area index ($\text{m}^2 \text{ m}^{-2}$). Comparisons among shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

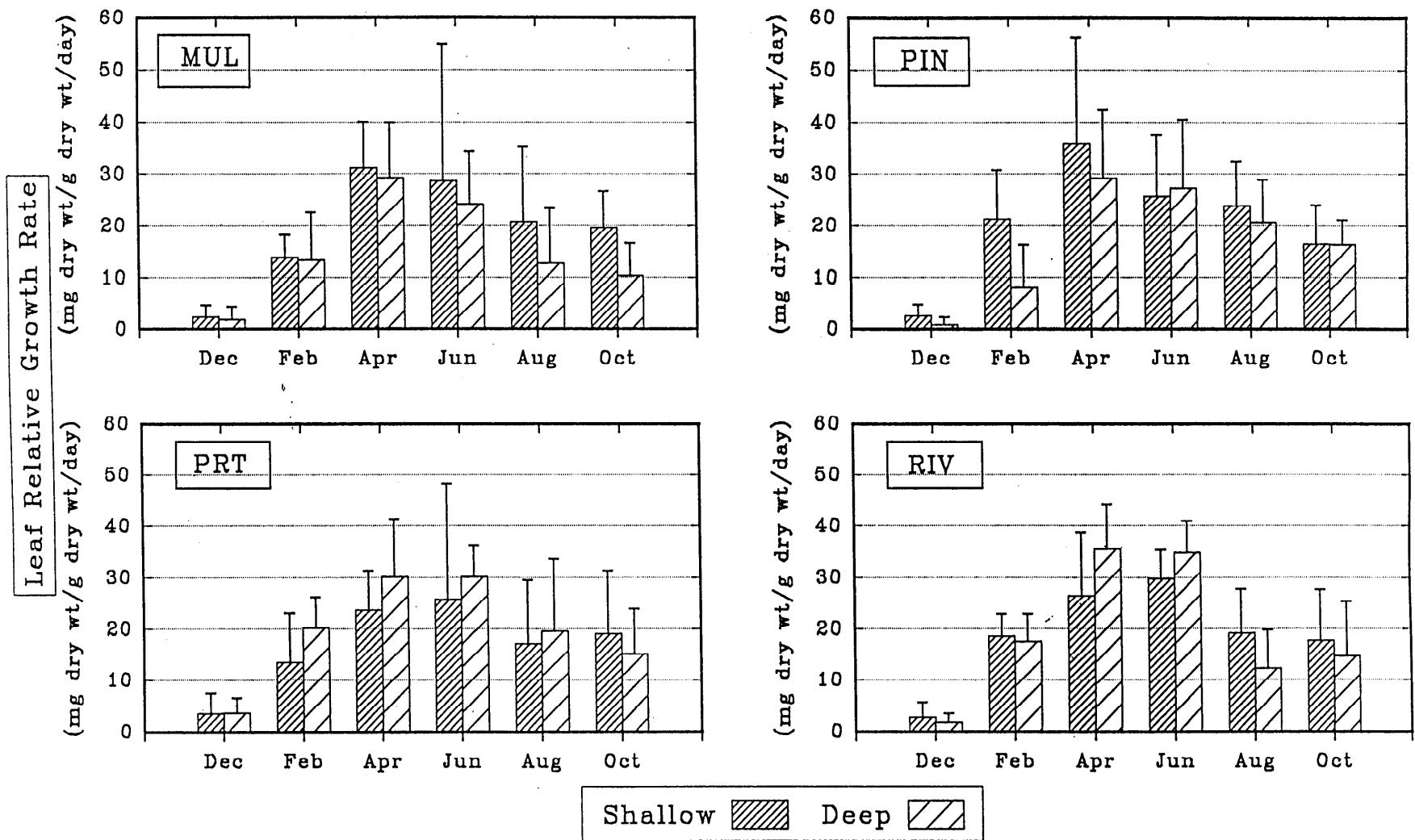


Figure 49. *Thalassia* leaf relative growth rate ($\text{mg dwt gdwt}^{-1} \text{ day}^{-1}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

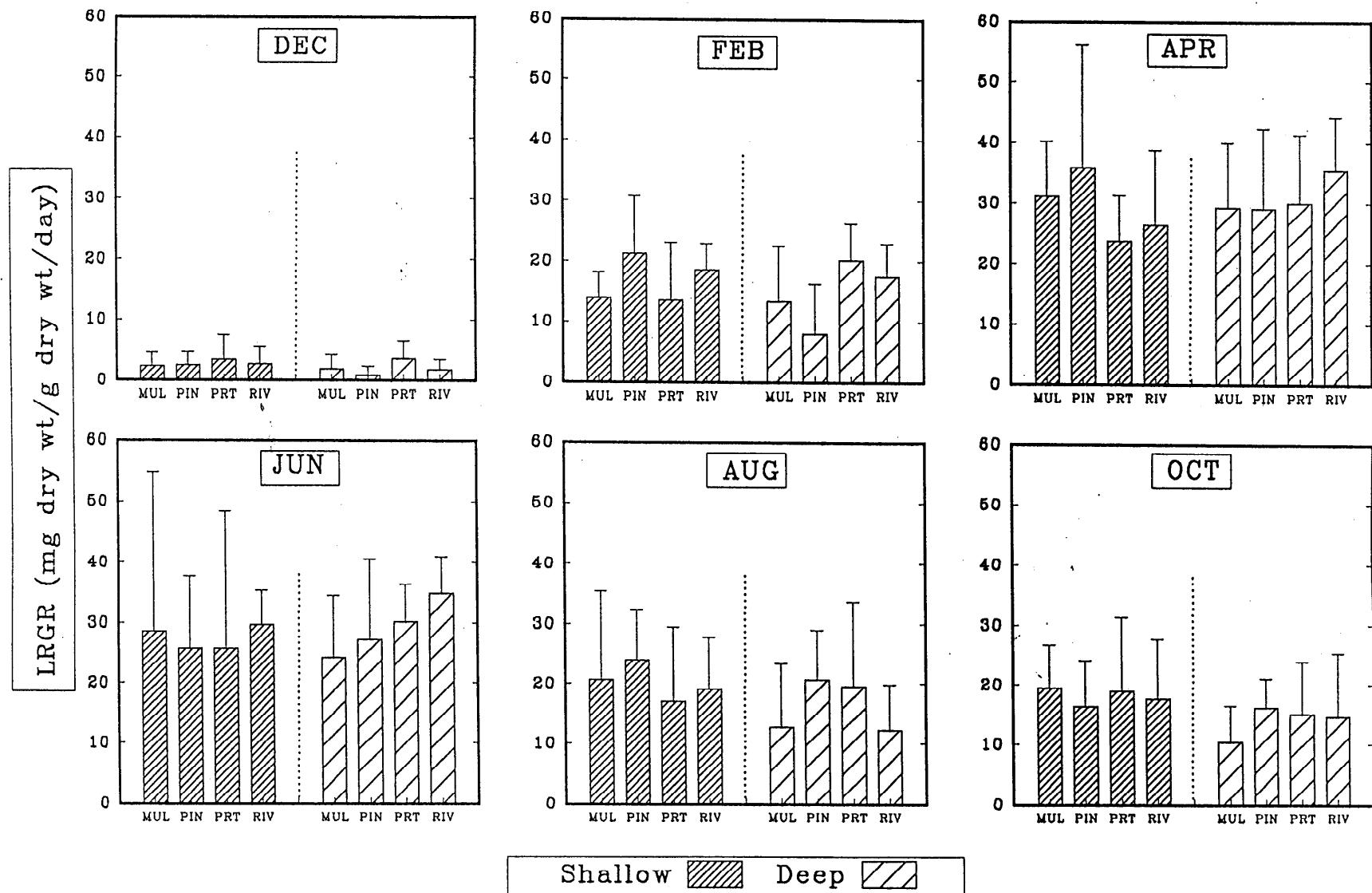


Figure 50. ***Thalassia*** leaf relative growth rate ($\text{mg dwt gdwt}^{-1} \text{ day}^{-1}$). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

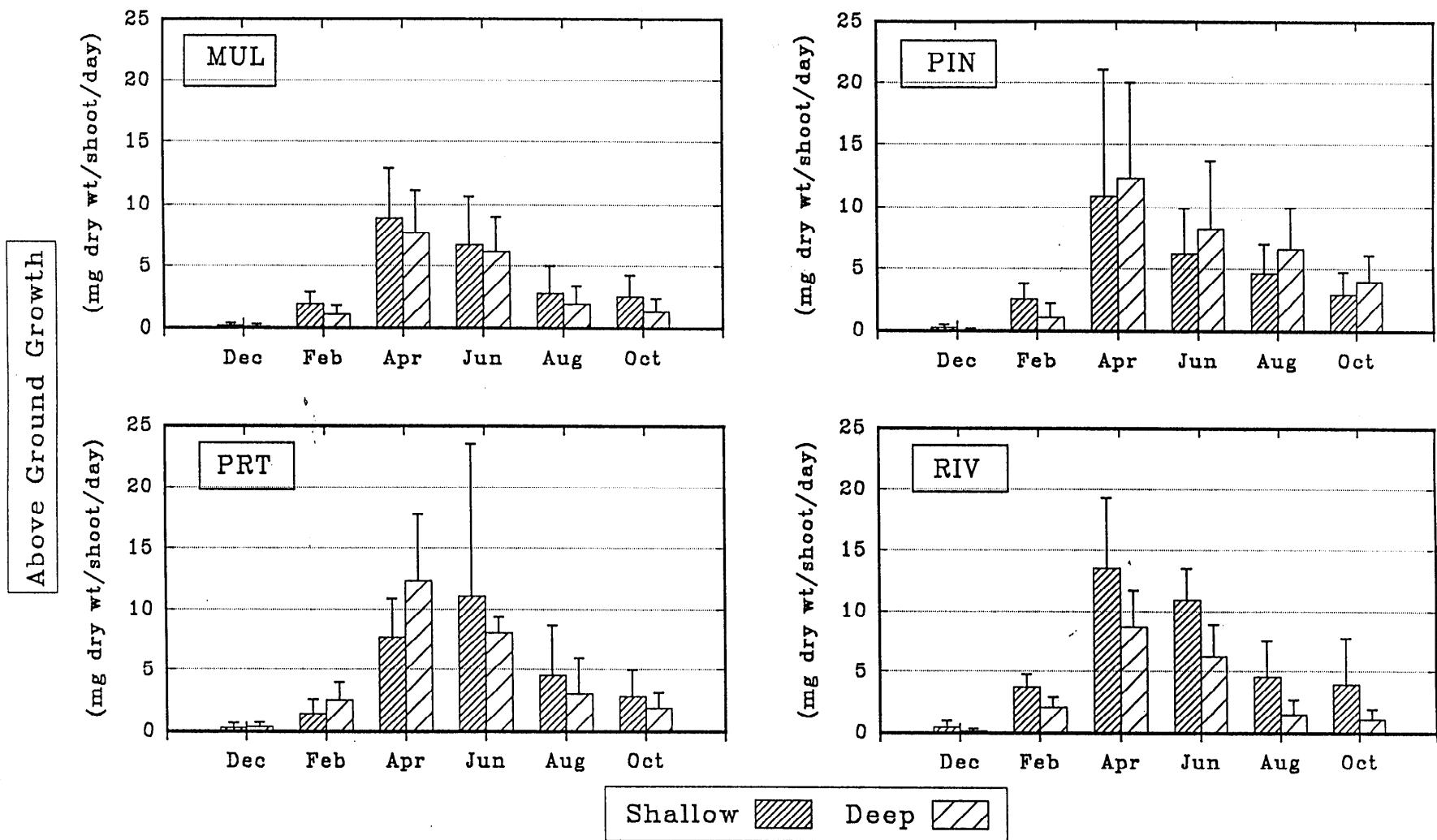


Figure 51. *Thalassia* blade production ($\text{mg dwt shoot}^{-1} \text{ day}^{-1}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

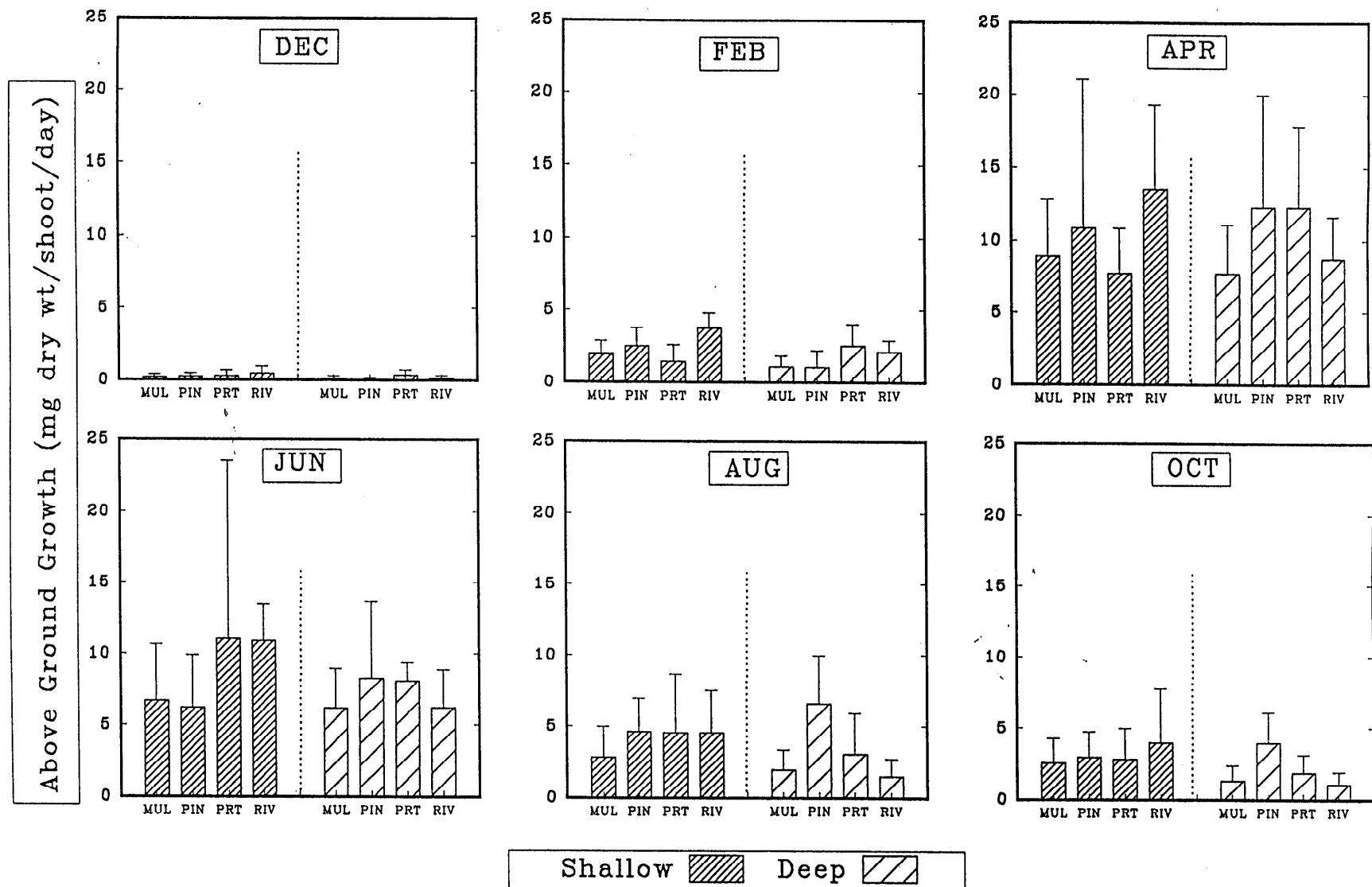


Figure 52. *Thalassia* blade production ($\text{mg dwt shoot}^{-1} \text{ day}^{-1}$). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

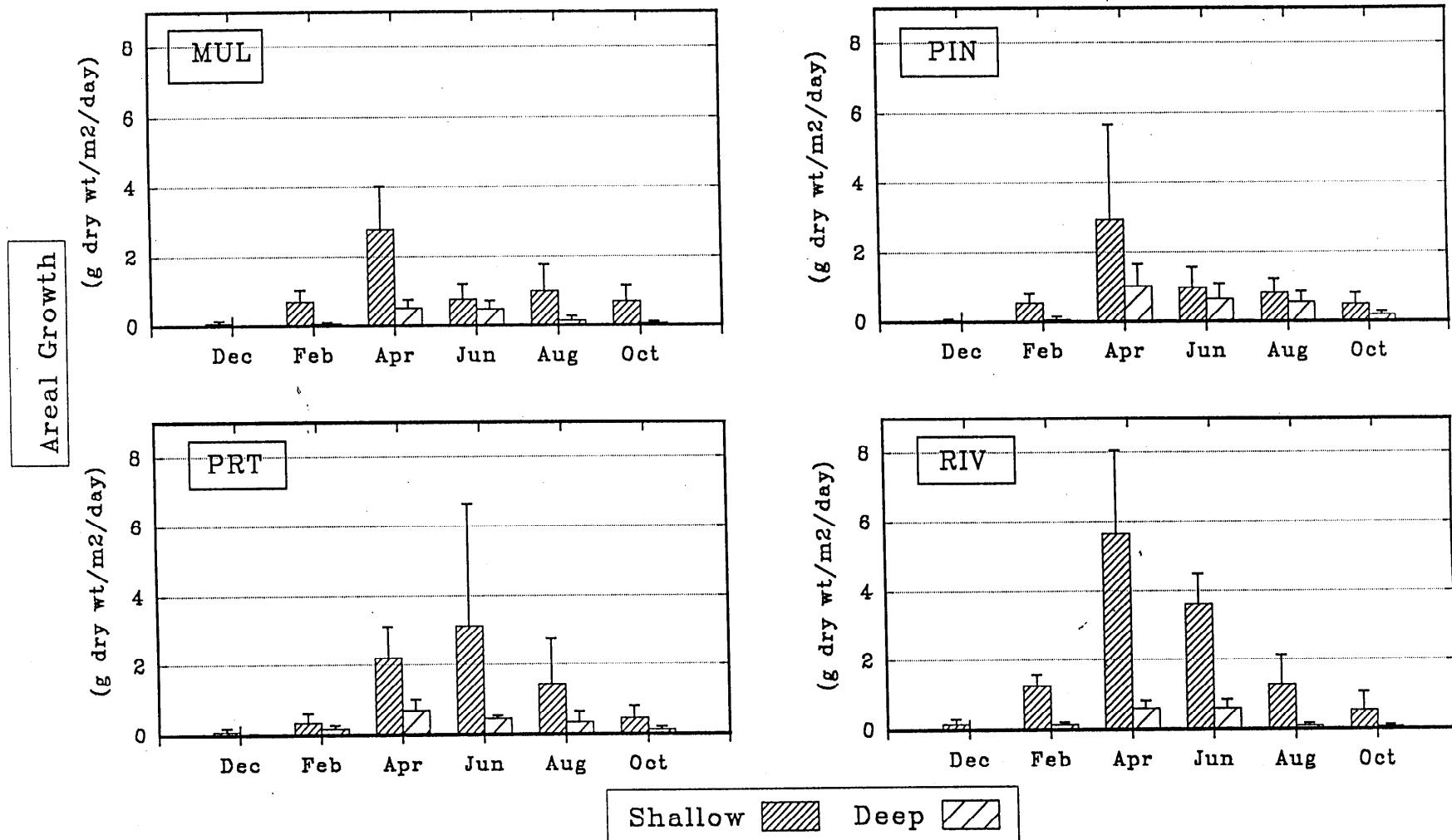


Figure 53. *Thalassia* areal growth ($\text{gdwt m}^{-2} \text{ day}^{-1}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

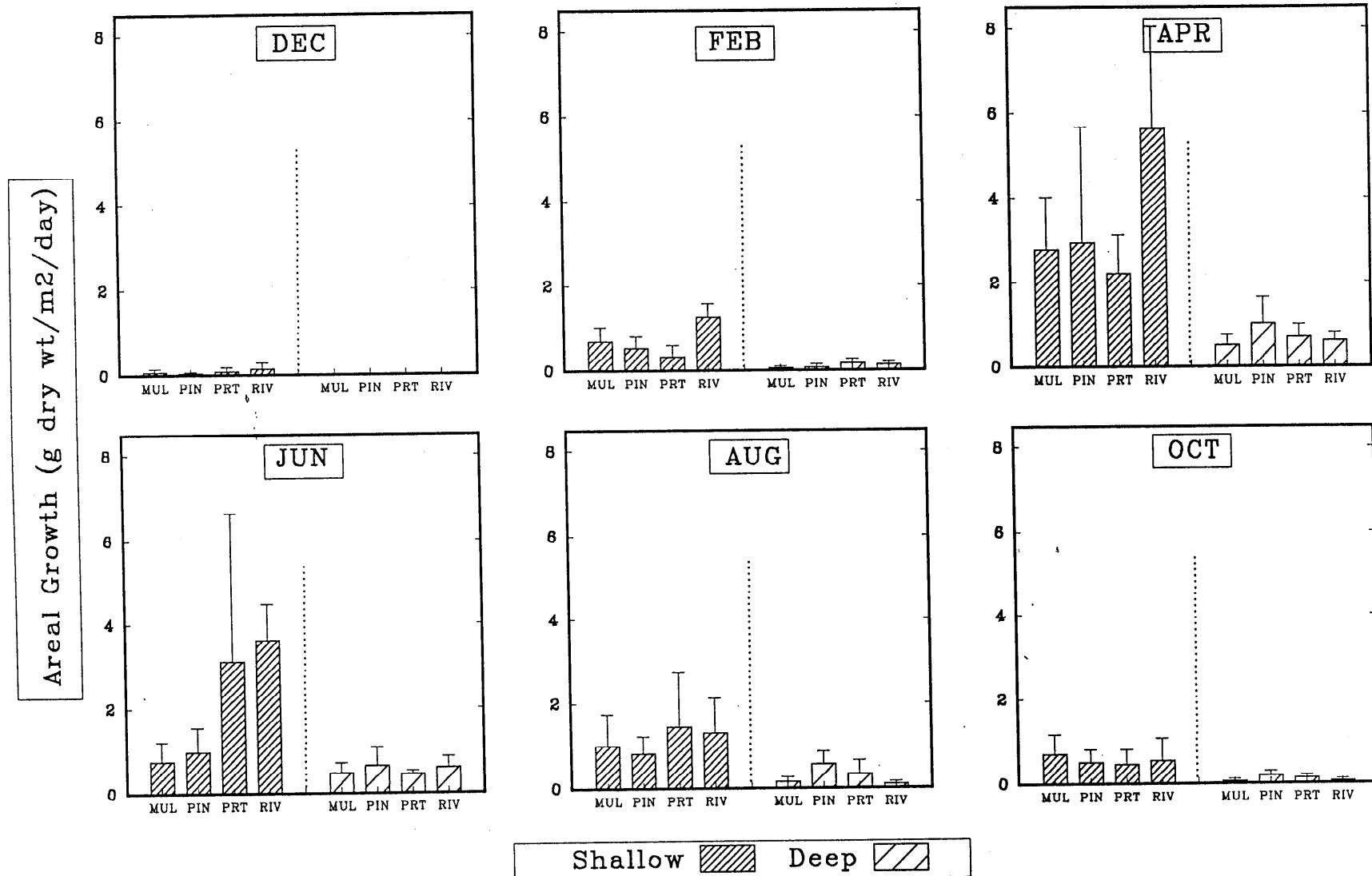


Figure 54. *Thalassia* areal growth ($\text{gdwt m}^{-2} \text{ day}^{-1}$). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 15$.

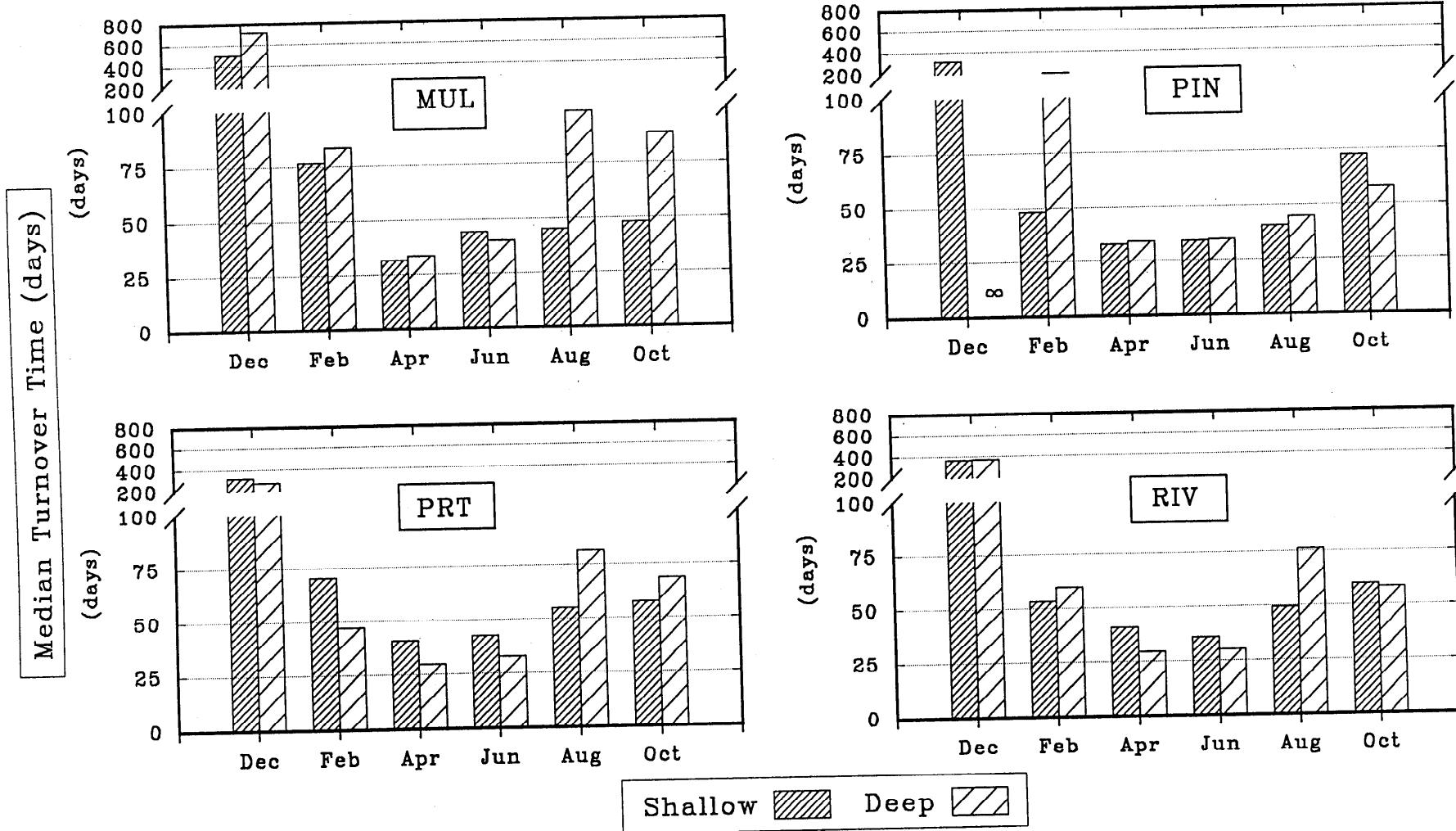


Figure 55. Median turnover time of *Thalassia* at shallow and deep stations for each of four sites from December 1993 through October 1994.

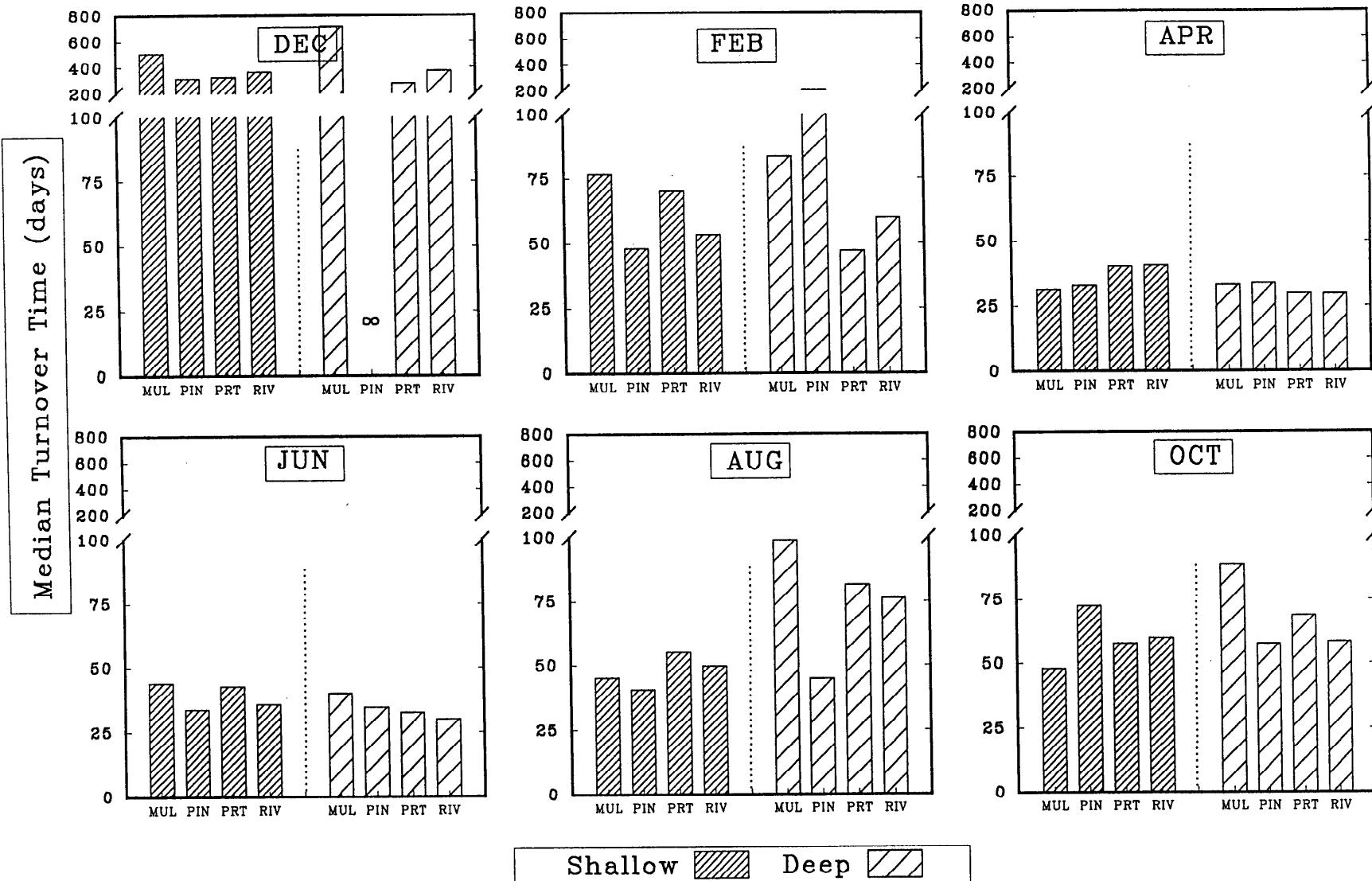


Figure 56. Median turnover time of *Thalassia*. Comparison among both shallow and deep stations at all sites from December 1993 through October 1994.

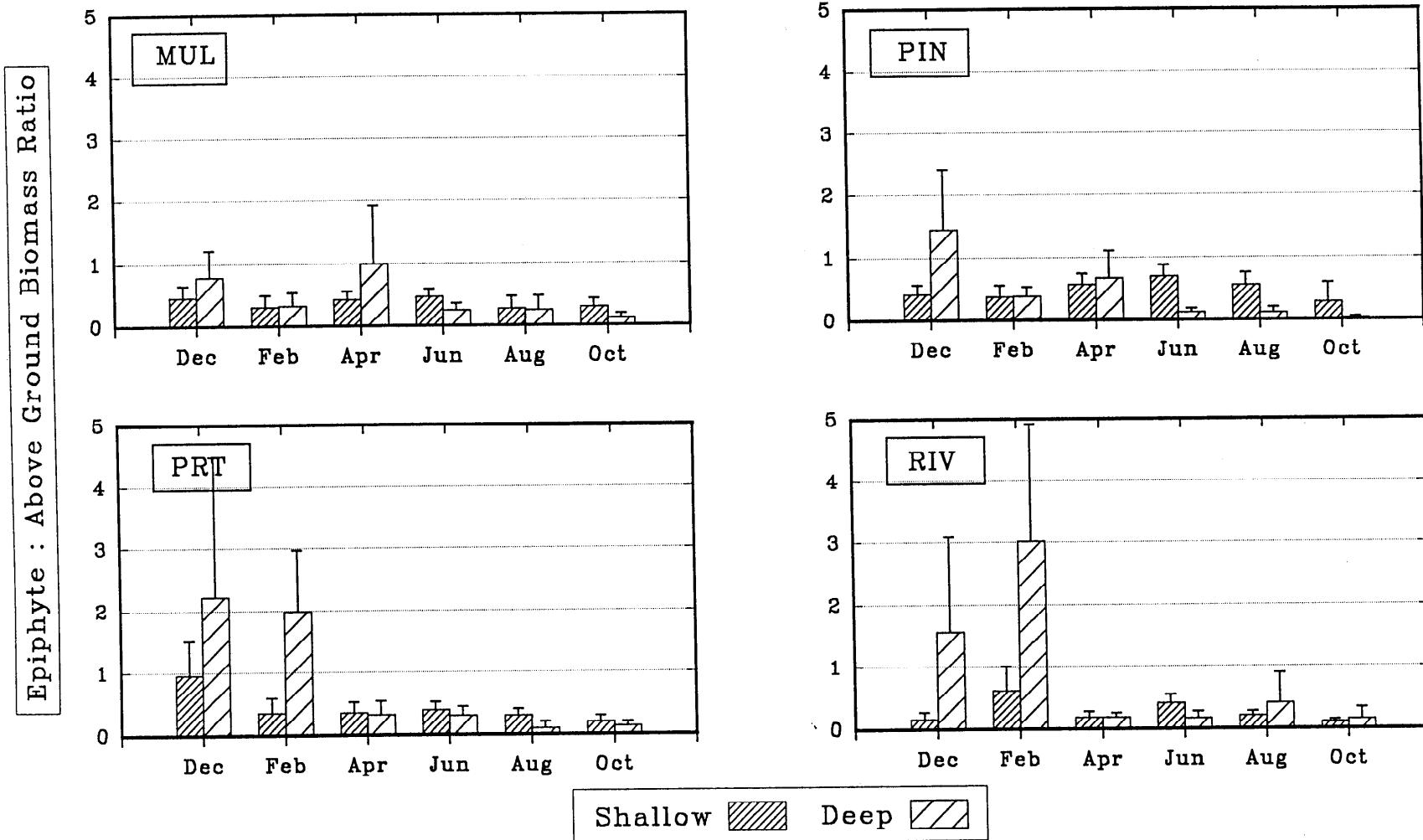


Figure 57. Ratio of epiphyte biomass to above-ground *Thalassia* biomass (blade weights) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10).

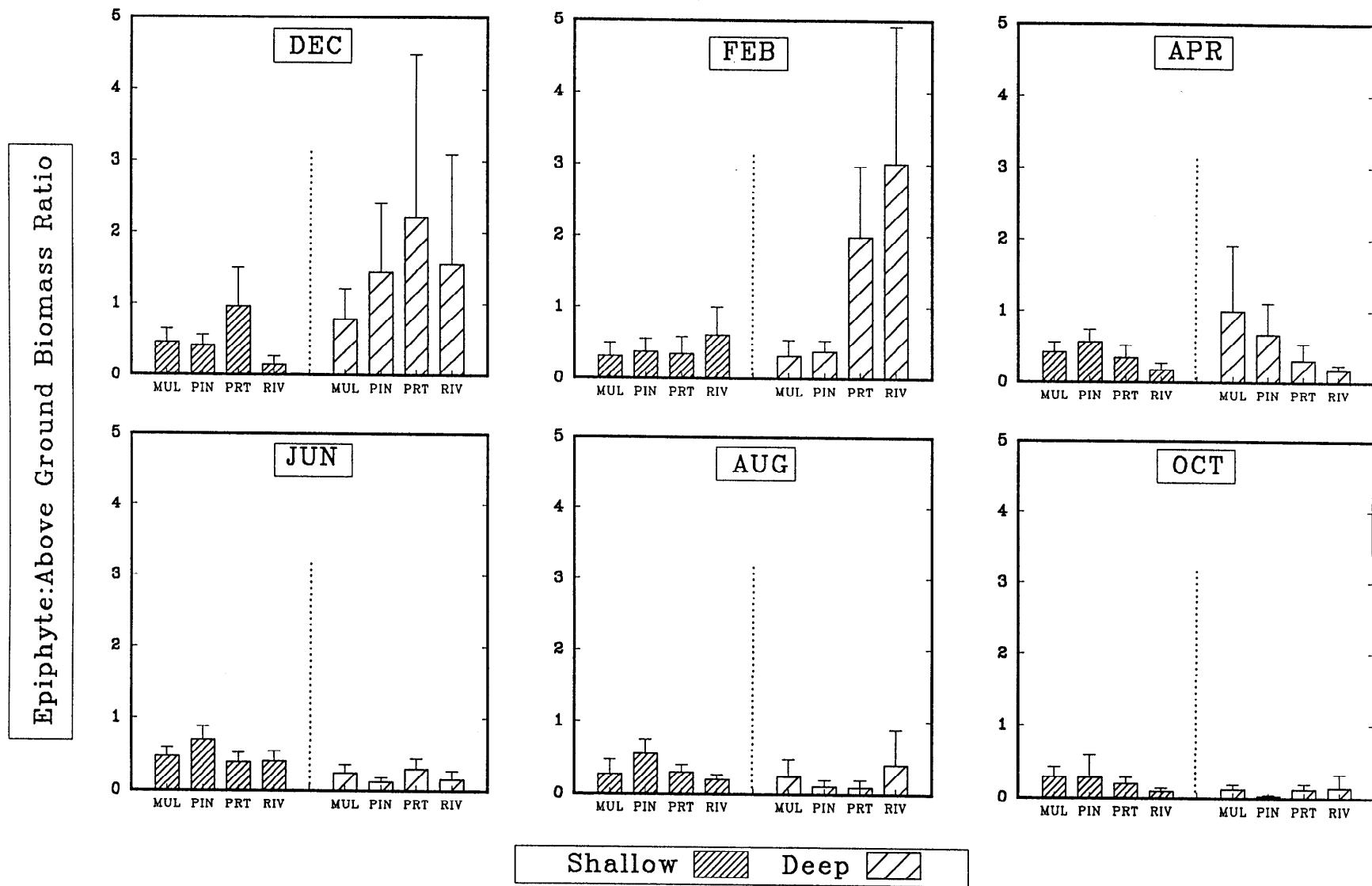


Figure 58. Ratio of epiphyte biomass to above-ground *Thalassia* biomass. Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10).

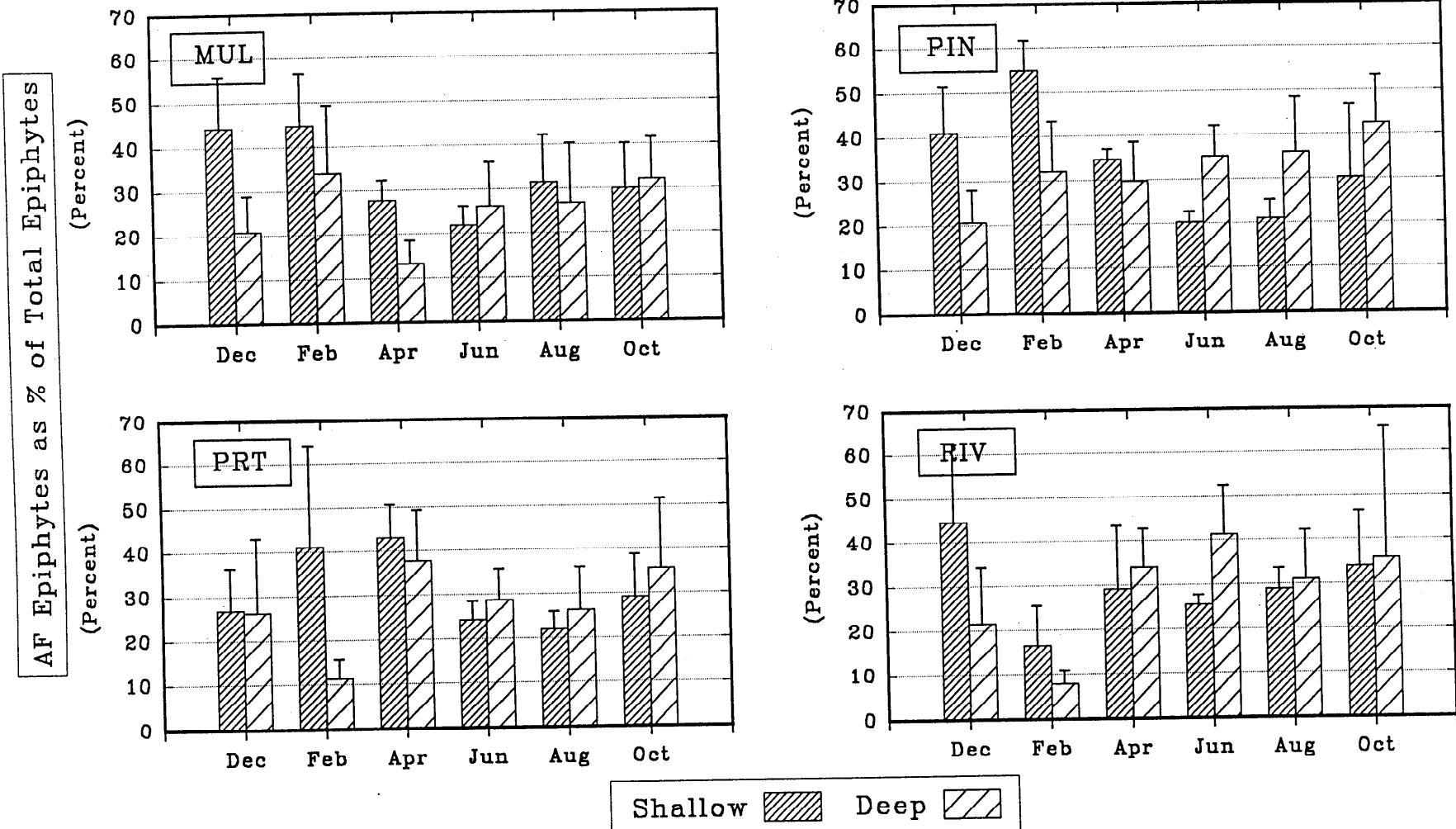


Figure 59. Ash-free epiphyte biomass as a percent of total epiphyte biomass at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 10$.

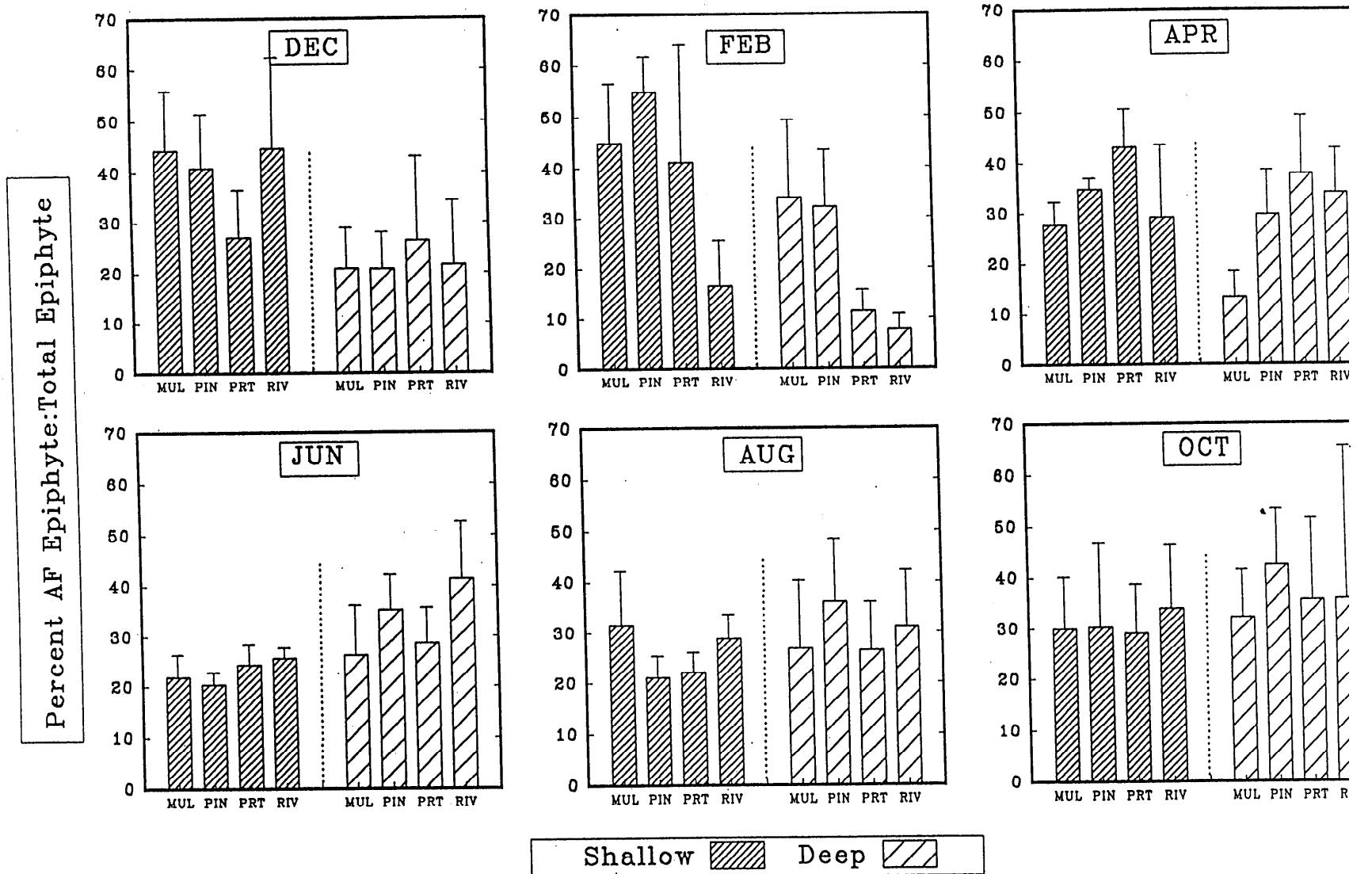


Figure 60. Ash-free epiphyte biomass as a percent of total epiphyte biomass. Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; n = 10).

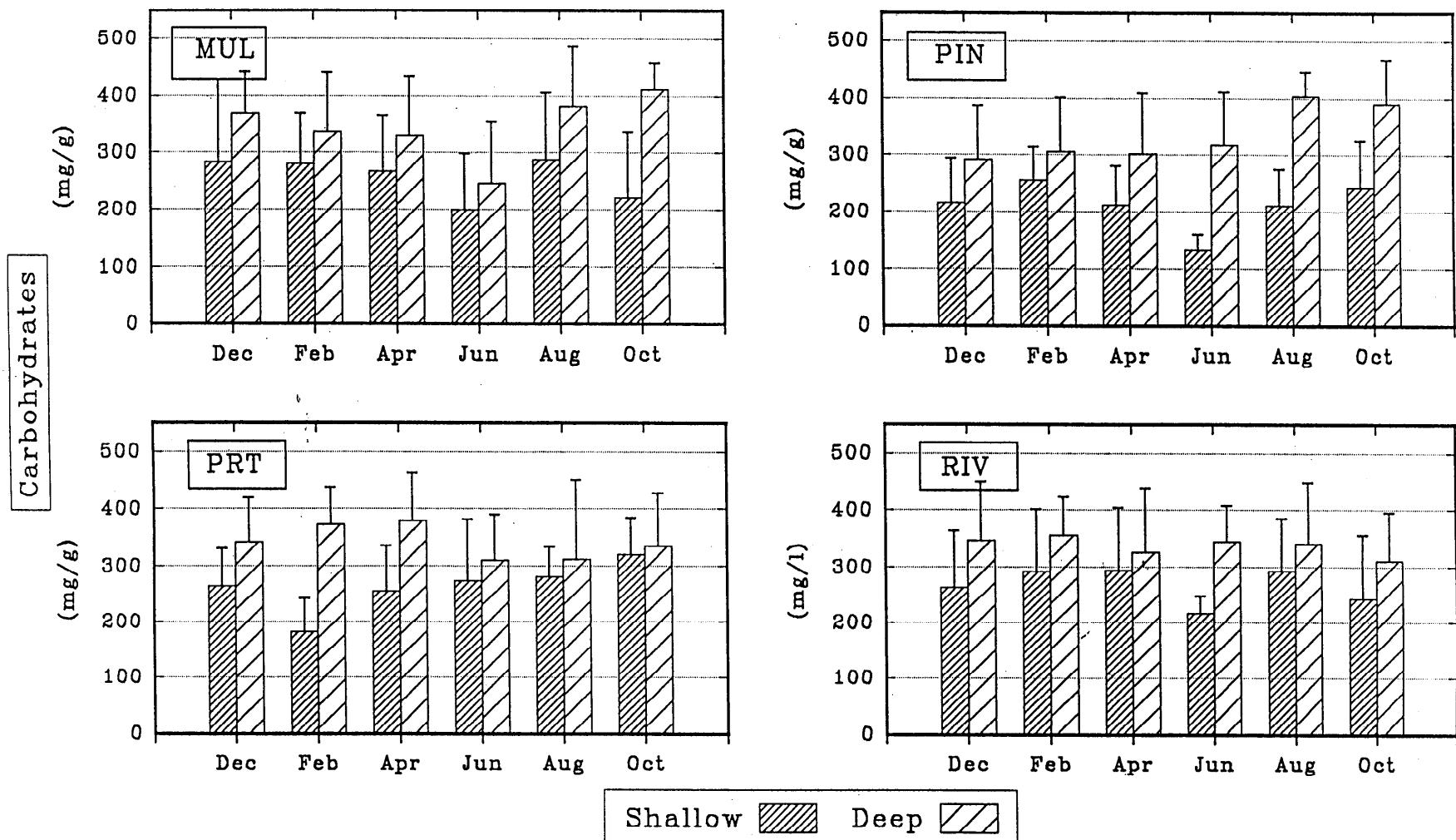


Figure 61. *Thalassia* rhizome soluble carbohydrate levels (mg gdwt^{-1}) at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 10$.

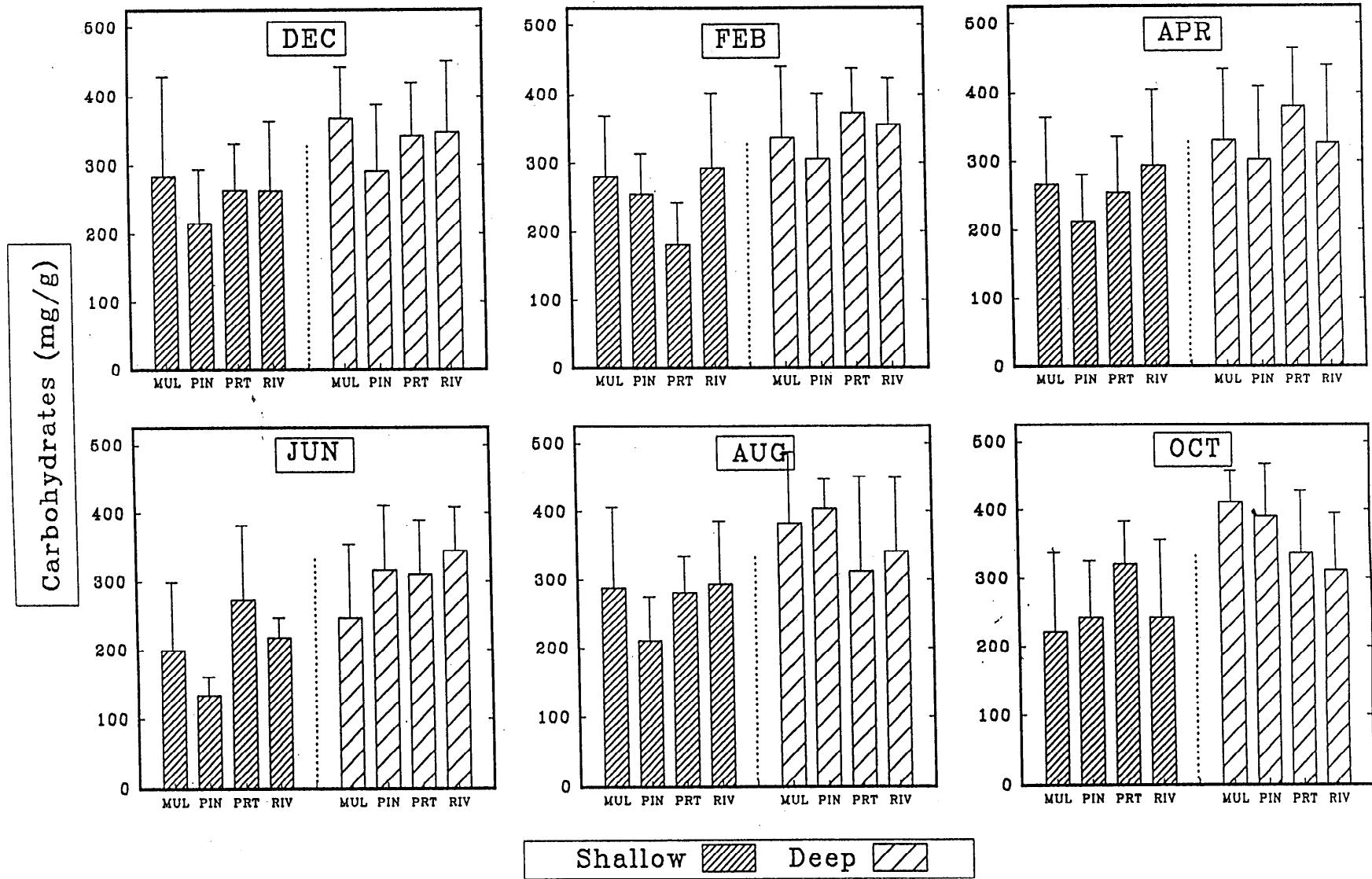


Figure 62. ***Thalassia*** rhizome soluble carbohydrate levels (mg gdwt^{-1}). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.; $n = 10$.

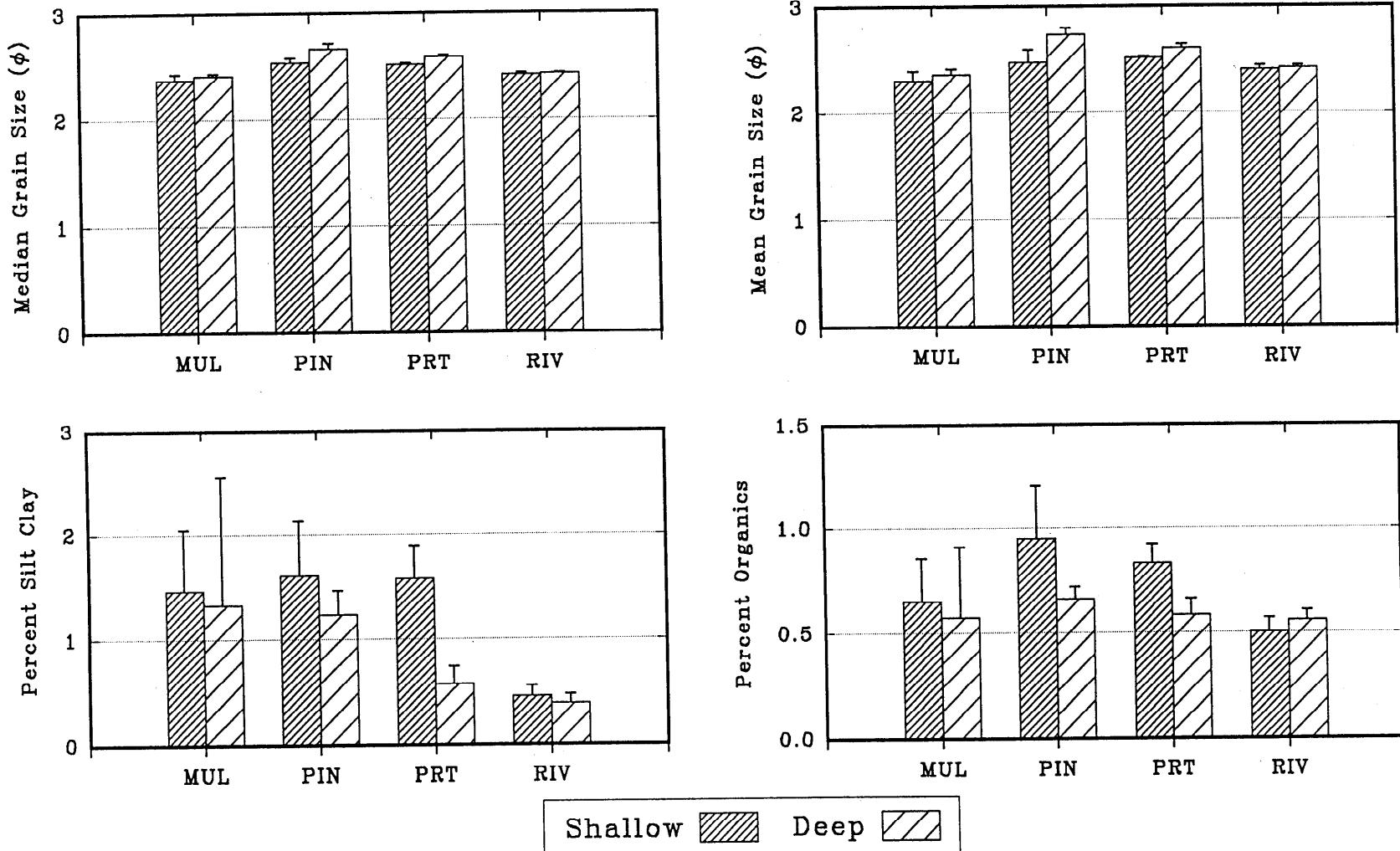


Figure 63. Sediment parameters at shallow and deep stations for each of four sites from January 1994. Values are means ± 1 s.d.; n = 5).

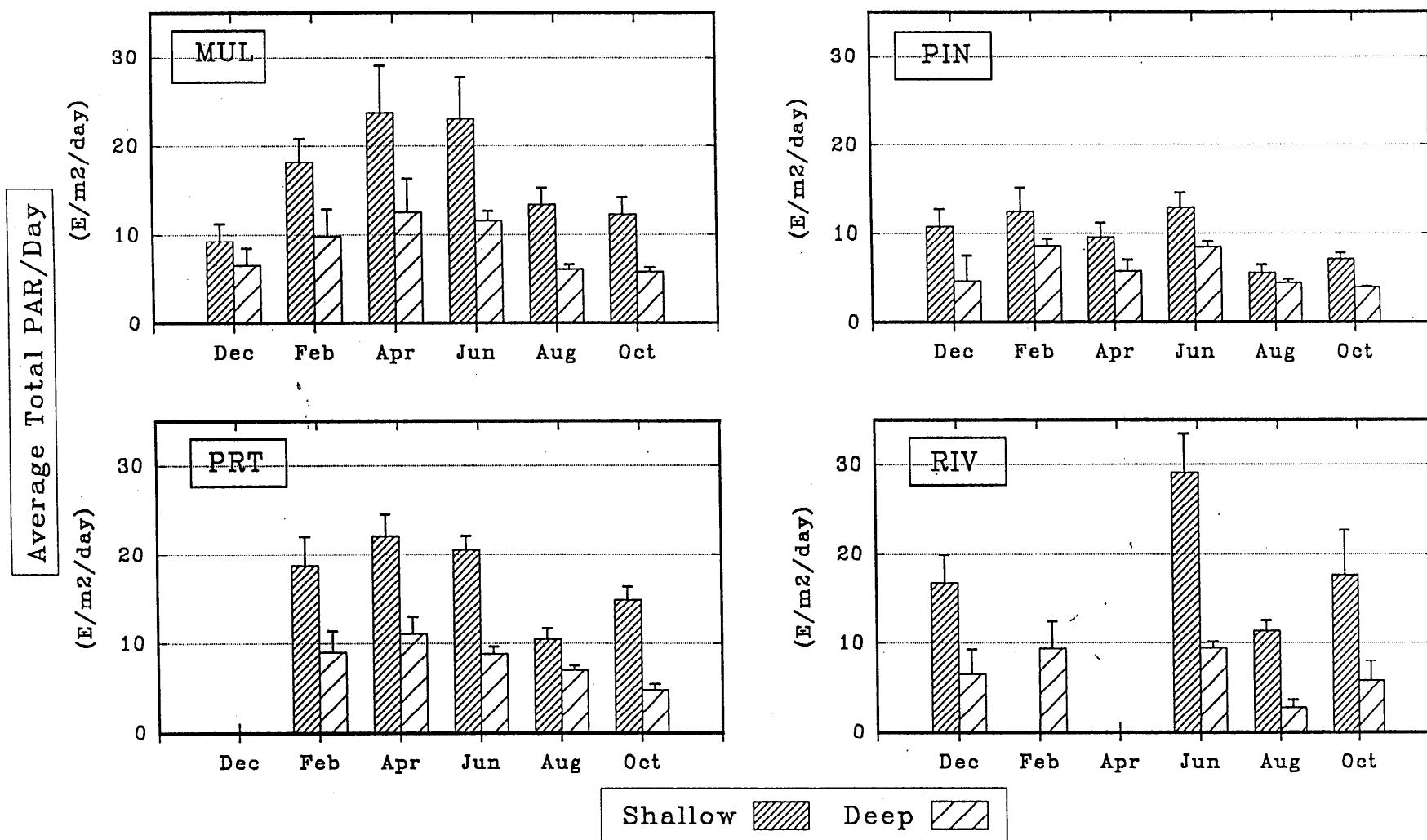


Figure 64. Average daily total PAR ($E\ m^{-2}\ day^{-1}$) for the two week period prior to *Thalassia* productivity measurements at shallow and deep stations for each of four sites from December 1993 through October 1994. Values are means ± 1 s.d.

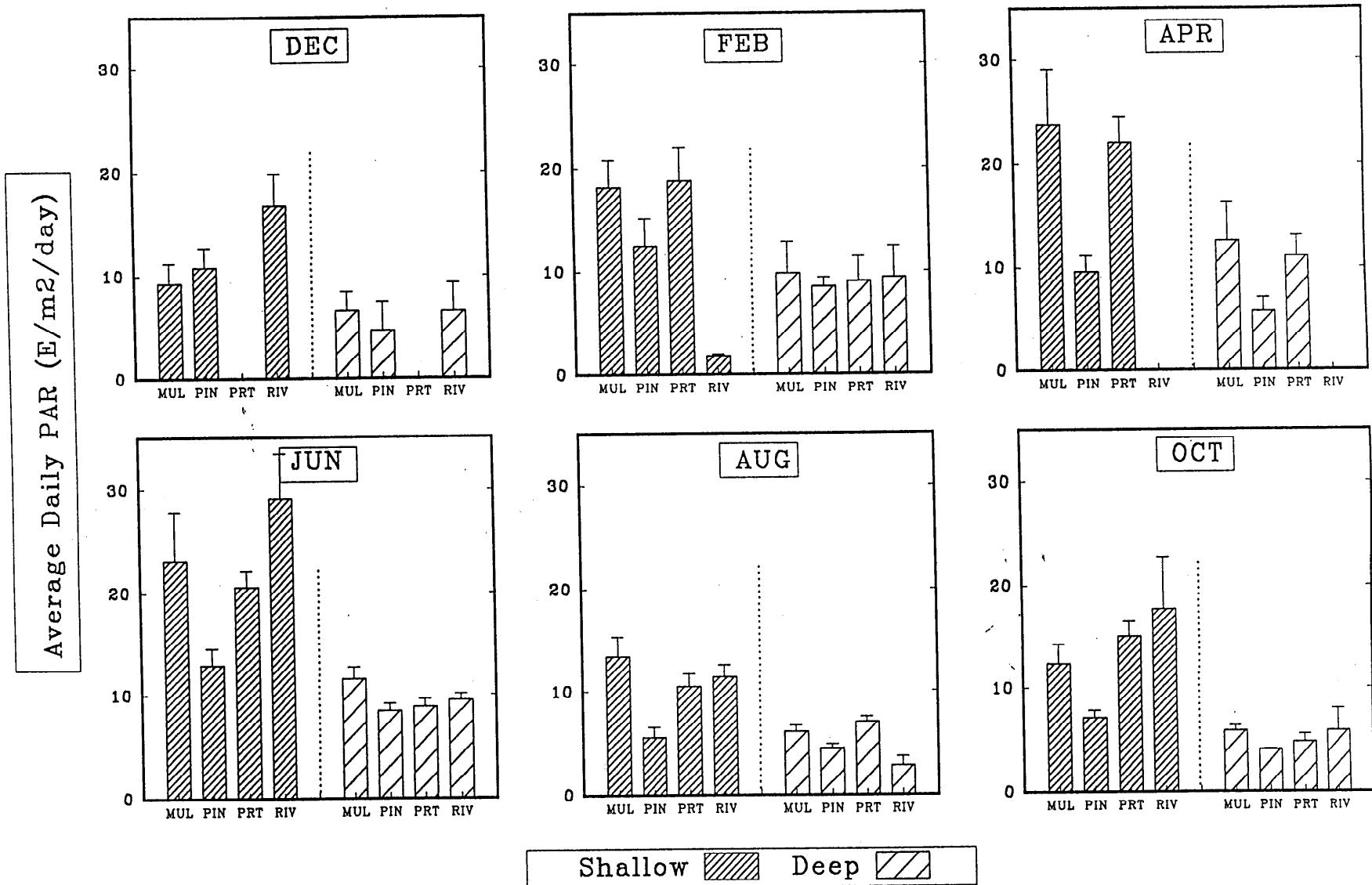


Figure 65. Average daily total PAR ($E m^{-2} day^{-1}$) for the two week period prior to *Thalassia* productivity measurements. Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. Values are means ± 1 s.d.

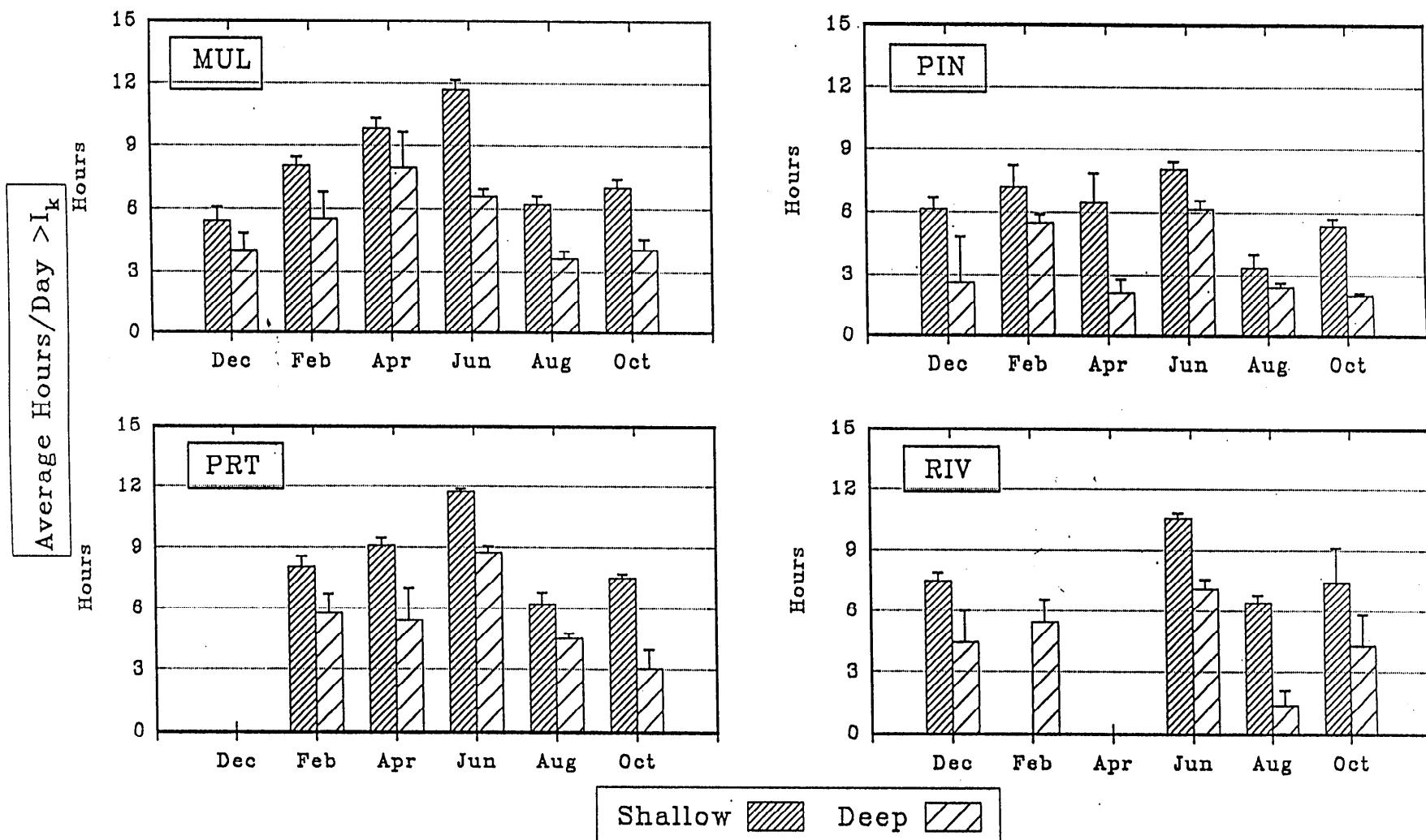


Figure 66. H_{sat} average number of hours per day that PAR ($\mu\text{E m}^{-2} \text{ sec}^{-1}$) was equal to or greater than saturating irradiance (E_k) at shallow and deep stations for each of 4 sites from December 1993 through October 1994. PAR levels adjusted for epiphyte attenuation. Values are means ± 1 s.d.

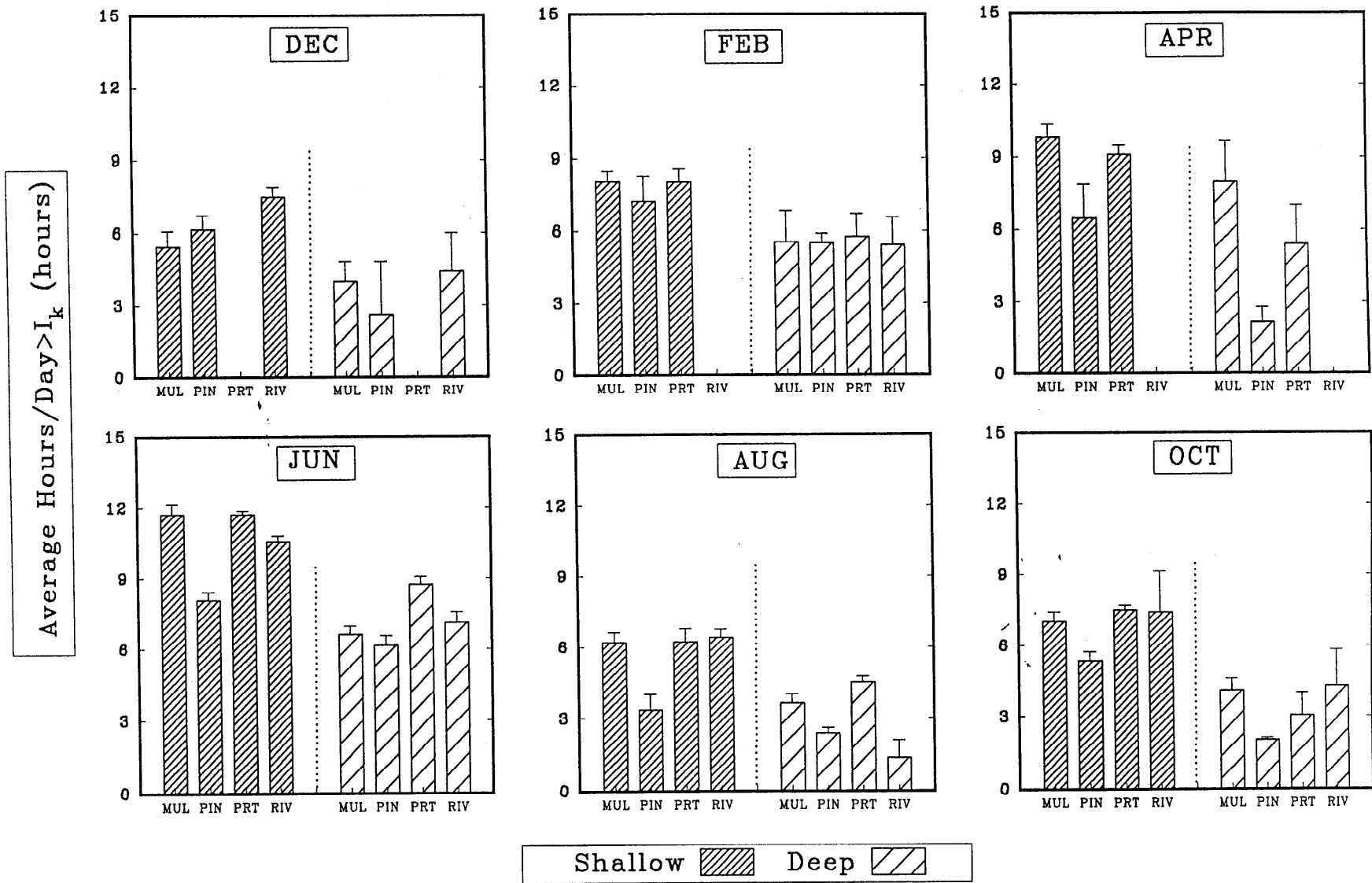


Figure 67. H_{sat} average number of hours per day that PAR ($\mu\text{E m}^{-2} \text{ sec}^{-1}$) was equal to or greater than saturating irradiance (E_k). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. PAR levels adjusted for epiphyte attenuation. Values are means ± 1 s.d.

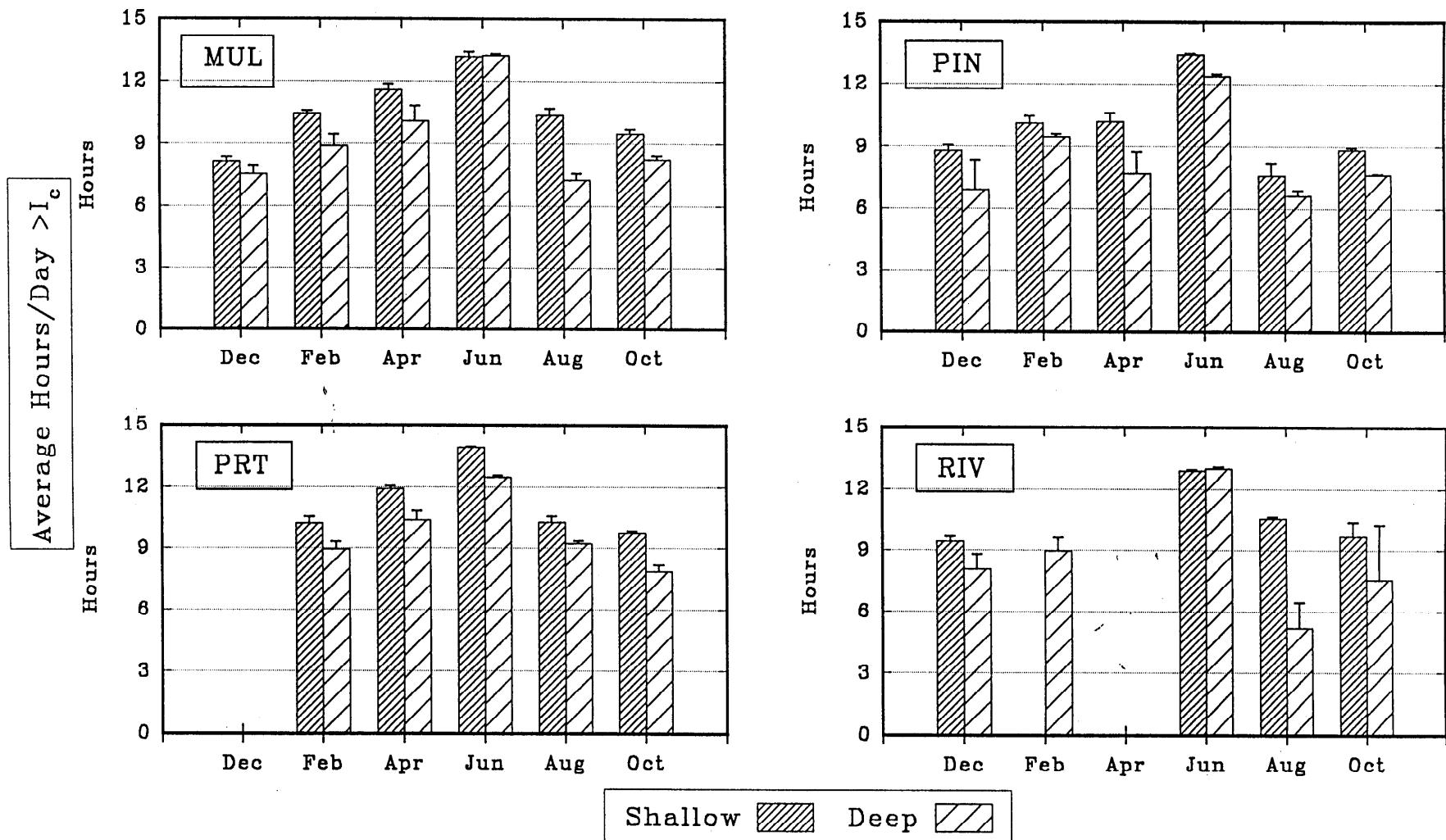


Figure 68. $H_{\text{comp-leaf}}$ average number of hours per day that PAR ($\mu\text{E m}^{-2} \text{ sec}^{-1}$) was equal to or greater than compensation irradiance for leaf tissue ($E_{\text{c-leaf}}$) at shallow and deep stations for each of four sites from December 1993 through October 1994. PAR levels adjusted for epiphyte attenuation. Values are means ± 1 s.d.

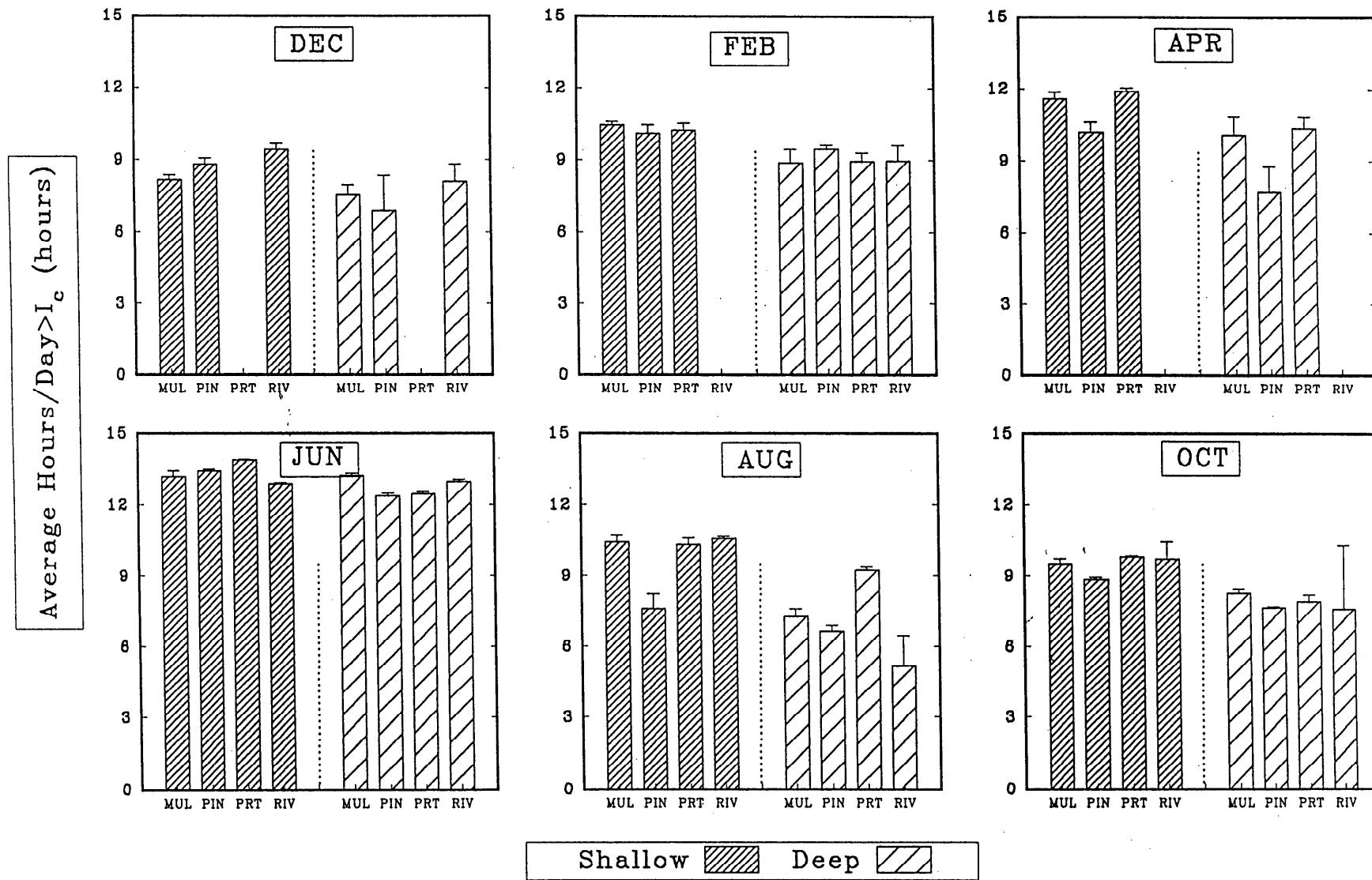


Figure 69. $H_{\text{comp-leaf}}$ average number of hours per day that PAR ($\mu\text{E m}^{-2} \text{ sec}^{-1}$) was equal to or greater than compensation irradiance for leaf tissue ($E_{c-\text{leaf}}$). Comparisons among both shallow and deep stations at all sites from December 1993 through October 1994. PAR levels adjusted for epiphyte attenuation. Values are means ± 1 s.d.

Table 1. Dates of *Thalassia* blade punching and retrieval at stations in Tampa Bay. Biomass cores collected when marked shoots recovered. Samplings referred to in text as December, February, April, June, August and October (consistent with marking dates) to emphasize bimonthly nature of sampling.

		MUL				PIN			
Punch	Deep Sample	Shallow Punch	Shallow Sample	Deep Punch	Sample	Shallow Punch	Shallow Sample		
12/20	01/05	12/20	01/05	12/20	01/10	12/20	01/05		
02/21	03/07	02/21	03/07	02/21	03/07	02/21	03/07		
04/25	05/02	04/25	05/02	04/25	05/02	04/25	05/02		
06/13	06/20	06/13	06/20	06/13	06/20	06/13	06/20		
08/08	08/16	08/08	08/16	08/08	08/16	08/08	08/16		
10/19	10/31	10/19	10/31	10/19	10/31	10/19	10/31		

		PRT				RIV			
Punch	Deep Sample	Shallow Punch	Shallow Sample	Deep Punch	Sample	Shallow Punch	Shallow Sample		
12/21	01/06	12/21	01/06	12/22	01/06	12/22	01/06		
02/22	03/08	02/22	03/08	02/22	03/08	02/21	03/08		
04/26	05/03	04/25	05/03	04/26	05/03	04/26	05/03		
06/14	06/21	06/13	06/21	06/14	06/21	06/14	06/21		
08/09	08/17	08/09	08/17	08/09	08/15	08/09	08/15		
10/19	11/01	10/19	11/01	10/20	11/01	10/20	11/01		

Table 2. Time periods of missing continuous light data.

Site	Date	Days	Sensors
MUL	January 27, 1994	21	both
	August 8, 1994	27	both
PIN	July 10, 1994	12	bottom
PRT	December 28, 1993	6	both
	January 9, 1994	11	bottom
	February 3, 1994	23	both
	July 26, 1994	14	both
RIV	March 8, 1994	13	top
	May 3, 1994	14	both
	September 24, 1994	5	both

Table 3. Annual mean Secchi depth for individual HCEPC stations, 1994.

<u>Station</u>	Hillsborough Bay	Middle Tampa Bay	Lower Tampa Bay		
	Secchi Depth (inches)	<u>Station</u>	Secchi Depth (inches)	<u>Station</u>	Secchi Depth (inches)
HCEPC 6	56	HCEPC 16	91	HCEPC 92	111
HCEPC 7	50	HCEPC 19	108	HCEPC 93	118
HCEPC 8	46	HCEPC 28	88	HCEPC 94	114
HCEPC 55	68	HCEPC 82	79	HCEPC 95	114
HCEPC 73	58	HCEPC 84	50	HCEPC 96	68
HCEPC 80	74				

Table 4. Water column attenuation coefficients measured at the maximum depth limits of *Thalassia* between 1000-1400 hours. (Monthly means except as noted.)

		MUL		PIN		PRT		RIV	
		Mean m ⁻¹	s.d. m ⁻¹						
1993	Dec	0.51	0.29	0.39	0.07	0.56	0.27	0.50	0.17
1994	Jan	0.74	0.31	0.72	0.26	ND	ND	0.57	0.21
	Feb	0.63	0.27	0.67	0.28	0.38	0.16	0.44	0.23
	Mar	0.76	0.54	0.62	0.23	0.52	0.48	0.47	0.23
	Apr	0.54	0.16	0.78	0.26	0.56	0.14	0.53	0.15
	May	0.63	0.19	1.04	1.04	0.75	0.27	0.61	0.18
	Jun	1.11	0.30	1.42	1.41	0.96	0.34	1.22	0.70
	Jul	1.02	0.17	0.73	0.11	0.81	0.17	1.07	0.23
	Aug	0.96	0.39	0.74	0.17	0.67	0.24	1.35	0.34
	Sep	1.14	0.15	0.88	0.17	1.28	0.24	1.59	0.37
	Oct	1.15	0.41	0.98	0.27	1.45	0.44	1.75	0.59
	Nov	0.85	0.27	0.65	0.18	1.27	0.51	1.19	0.32
Annual									
Mean of months		0.84		0.80		0.84		0.94	
Mean all data		0.83		0.80		0.86		0.98	
s.d. all data		0.39		0.58		0.48		0.58	
25 th Percentile		0.56		0.54		0.48		0.51	
50 th Percentile		0.76		0.73		0.78		0.88	
75 th Percentile		1.05		0.89		1.12		1.31	
Growing Season (May-Sept)									
Mean of months		0.97		0.96		0.89		1.17	
Mean of all data		0.96		0.96		0.90		1.16	
s.d. of all data		0.33		0.83		0.35		0.52	
25 th Percentile		0.73		0.69		0.66		0.78	
50 th Percentile		0.95		0.79		0.86		1.12	
75 th Percentile		1.16		0.92		1.10		1.44	

Table 5. Mean water depths and approximate elevations of the maximum depth limits of *Thalassia*.

	Mean Water Depth (m)	Elevation of Deep Edge (m below MLLW)
MUL	2.10	1.76
PIN	2.37	2.04
PRT	2.15	1.81
RIV	1.98	1.63

Table 6. Percentage of PAR at the maximum depth limits of ***Thalassia*** from data collected between 1000-1400 hours. Computed with fixed and tidally varying station depths.

MUL			PIN			PRT			RIV		
	% PAR Available 1000-1400 hrs	Fixed Depth Tidal		% PAR Available 1000-1400 hrs	Fixed Depth Tidal		% PAR Available 1000-1400 hrs	Fixed Depth Tidal		% PAR Available 1000-1400 hrs	Fixed Depth Tidal
1993	Dec	39.8	42.4	40.1	43.0	33.6	37.6	38.7	39.9		
1994	Jan	24.8	28.1	21.6	23.8	ND	ND	34.4	34.6		
	Feb	30.0	30.9	23.6	24.9	46.4	47.6	46.0	45.3		
	Mar	27.4	26.9	25.5	25.7	41.0	41.0	42.7	40.3		
	Apr	33.9	32.0	18.8	18.1	32.0	30.6	36.3	33.8		
	May	28.3	25.9	20.4	19.1	22.6	21.4	31.1	28.4		
	Jun	11.5	10.2	11.4	10.0	14.8	14.2	14.4	13.4		
	Jul	12.6	10.6	18.3	17.6	18.5	18.7	13.3	12.7		
	Aug	16.4	16.4	18.8	18.4	27.1	28.0	8.4	8.2		
	Sep	9.7	10.2	13.4	14.0	7.0	8.2	5.4	5.9		
	Oct	11.2	12.7	11.2	12.4	6.4	7.9	4.7	5.5		
	Nov	19.3	21.6	22.8	25.2	9.3	11.5	11.2	12.6		
Annual											
	Mean of months	22.1	22.3	20.5	21.0	23.5	24.2	23.9	23.4		
	Mean all data	22.6	22.8	20.6	21.2	23.0	23.7	22.5	22.1		
	s.d. all data	14.4	14.7	11.2	11.9	16.4	16.3	17.4	17.1		
	25 th Percentile	11.0	10.6	12.2	11.6	9.0	10.2	7.4	7.4		
	50 th Percentile	20.2	20.0	17.7	17.3	18.8	19.2	17.4	17.2		
	75 th Percentile	30.8	32.5	27.8	27.3	35.7	35.5	36.4	34.8		
Growing Season (May-Sept)											
	Mean of months	15.7	14.6	16.4	15.8	18.0	18.1	14.5	13.7		
	Mean of all data	16.3	15.3	16.5	16.0	18.1	18.1	14.6	13.8		
	s.d. of all data	10.0	9.8	7.8	7.7	11.5	11.4	11.1	10.5		
	25 th Percentile	8.8	7.7	11.3	10.8	9.4	9.7	6.1	5.6		
	50 th Percentile	13.6	13.5	15.4	14.7	15.8	15.5	10.8	10.7		
	75 th Percentile	21.6	20.3	19.5	19.2	24.3	24.6	19.6	19.9		

Table 7. Epiphytic attenuation of PAR due to epiphytic load measured on individual shoots of *Thalassia*. Units are % attenuation.

	MUL				PIN				PRT				RIV			
	Deep Mean	s.d.	Shallow Mean	s.d.												
Dec	47.8	14.6	57.0	8.9	64.6	21.1	50.7	8.8	67.3	19.1	62.0	12.0	52.4	19.8	24.4	13.8
Feb	32.4	20.7	34.1	9.4	40.2	5.9	46.7	11.4	47.7	13.8	26.6	12.6	54.3	14.7	23.9	6.9
Apr	50.6	14.9	46.3	12.0	42.2	13.4	56.4	7.1	39.3	11.0	44.1	6.1	24.1	4.1	21.1	7.4
Jun	22.9	7.6	41.8	11.9	20.1	6.5	50.9	6.1	30.1	6.1	35.5	4.8	22.8	5.2	36.9	9.3
Aug	21.8	8.0	38.9	8.7	18.1	7.2	49.2	8.8	10.8	6.3	30.8	8.1	33.6	20.5	27.6	7.1
Oct	20.2	7.3	32.0	10.2	6.7	1.7	26.3	6.9	22.2	11.7	21.4	7.5	17.8	29.6	25.1	20.9
Annual Mean	32.6		41.7		32.0		46.7		36.2		36.7		34.2		26.5	

Table 8. Percentage of PAR available to ***Thalassia*** at maximum depth limits computed from water column attenuation coefficients and epiphytic attenuation, fixed water volume depths and data collected between 1000-1400 hours.

		MUL		PIN		PRT		RIV			
		% PAR Available to Plant	Mean	% PAR Available to Plant	Mean	s.d.	% PAR Available to Plant	Mean	s.d.	% PAR Available to Plant	Mean
1993	Dec	20.8	10.0	14.2	2.4		11.0	4.0		18.4	5.1
1994	Jan	13.0	6.2	7.6	4.0		ND	4.0		16.4	5.0
	Feb	19.3	16	12.6	6.2		24.0	6.7		21.2	9.4
	Mar	18.0	8.3	15.2	6.1		21.5	7.6		19.5	6.2
	Apr	17.7	7.5	11.0	6.9		18.7	4.8		24.9	8.3
	May	14.8	4.7	12.6	6.2		14.1	6.3		23.7	6.4
	Jun	8.9	4.4	9.1	3.6		10.3	4.1		11.1	7.1
	Jul	9.7	3.3	14.9	3.7		14.6	6.2		9.8	5.1
	Aug	12.9	5.6	15.4	6.0		24.2	12.8		5.6	3.3
	Sep	7.6	2.2	11.4	4.4		6.1	2.3		3.8	2.7
	Oct	8.9	4.1	10.4	4.2		5.0	4.4		4.3	3.2
	Nov	15.4	6.9	21.3	6.8		7.2	4.7		10.2	5.1
<hr/>											
Annual											
Mean of months		13.9		13.0			14.2			14.1	
Mean all data		14.3		13.0			14.2			13.4	
s.d. all data		7.8		6.3			9.5			9.0	
25 th Percentile		8.2		8.4			6.9			5.5	
50 th Percentile		13.1		12.3			12.4			12.1	
75 th Percentile		18.6		16.6			20.8			20.3	
<hr/>											
Growing Season (May-Sept)											
Mean of months		10.8		12.7			13.8			10.8	
Mean of all data		10.9		12.7			13.9			10.9	
s.d. of all data		5.2		5.5			9.7			8.6	
25 th Percentile		6.9		8.8			7.3			4.0	
50 th Percentile		10.2		12.0			11.1			7.7	
75 th Percentile		14.6		15.3			18.1			16.1	

Table 9. Absolute PAR levels recorded ***Thalassia*** at maximum depth limits. Monthly values of maximum observed PAR, average PAR (during daylight hours), and average daily total PAR.

	MUL			PIN			PRT			RIV		
	Maximum PAR μE m ⁻¹ sec ⁻¹	Average PAR μE m ⁻¹ sec ⁻¹	Average Daily Total PAR E m ⁻² day ⁻¹	Maximum PAR μE m ⁻¹ sec ⁻¹	Average PAR μE m ⁻¹ sec ⁻¹	Average Daily Total PAR E m ⁻² day ⁻¹	Maximum PAR μE m ⁻¹ sec ⁻¹	Average PAR μE m ⁻¹ sec ⁻¹	Average Daily Total PAR E m ⁻² day ⁻¹	Maximum PAR μE m ⁻¹ sec ⁻¹	Average PAR μE m ⁻¹ sec ⁻¹	Average Daily Total PAR E m ⁻² day ⁻¹
Dec	1281	404	16.3	991	339	15.0	1048	367	11.6	982	348	13.6
Jan	1349	150	5.6	1190	271	10.8				1044	310	13.6
Feb	1144	340	14.9	2314	270	11.5	1285	413	18.1	1549	416	19.2
Mar	1380	426	19.1	1168	360	16.1	1371	503	23.6	1589	555	25.9
Apr	1438	522	24.5	1206	289	13.8	1301	496	22.7	1372	491	23.5
May	1329	437	21.1	1231	331	15.7	1102	399	19.0	1325	460	23.4
Jun	1057	252	12.2	778	179	7.6	1034	232	11.4	1039	237	11.9
Jul	1004	235	10.7	856	207	6.7	914	217	10.1	726	194	9.6
Aug	1032	295	14.3	703	192	8.9	953	271	12.7	839	152	6.6
Sep	658	175	8.0	540	110	4.8	623	164	7.2	473	91	3.5
Oct	521	137	5.9	290	83	3.4	468	112	4.6	522	108	4.1
Nov	562	185	7.3	428	139	5.5	524	152	6.0	684	190	7.4
Annual Average Daily PAR (E m ⁻² day ⁻¹)		13.3			10.0				13.4			13.5
Annual Total PAR (E year ⁻¹)		4,864			3,639				4,876			4,934

Table 10. Absolute PAR levels recorded at *Thalassia* maximum depths limits after water column and epiphytic attenuation. Monthly values of maximum observed PAR, average PAR (during daylight hours), and average daily total PAR.

	MUL			PIN			PRT			RIV		
	Maximum PAR	Average PAR	Average Daily Total PAR	Maximum PAR	Average PAR	Average Daily Total PAR	Maximum PAR	Average PAR	Average Daily Total PAR	Maximum PAR	Average PAR	Average Daily Total PAR
	$\mu\text{E m}^{-1} \text{ sec}^{-1}$	$\mu\text{E m}^{-1} \text{ sec}^{-1}$	$\text{E m}^{-2} \text{ day}^{-1}$	$\mu\text{E m}^{-1} \text{ sec}^{-1}$	$\mu\text{E m}^{-1} \text{ sec}^{-1}$	$\text{E m}^{-2} \text{ day}^{-1}$	$\mu\text{E m}^{-1} \text{ sec}^{-1}$	$\mu\text{E m}^{-1} \text{ sec}^{-1}$	$\text{E m}^{-2} \text{ day}^{-1}$	$\mu\text{E m}^{-1} \text{ sec}^{-1}$	$\mu\text{E m}^{-1} \text{ sec}^{-1}$	$\text{E m}^{-2} \text{ day}^{-1}$
Dec	669	211	8.5	351	125	5.3	343	124	3.8	467	167	6.5
Jan	704	78	2.9	421	97	3.8				497	154	6.5
Feb	754	219	9.6	819	145	6.1	672	211	9.2	708	194	8.8
Mar	910	281	12.6	699	216	9.6	717	263	12.3	726	258	11.8
Apr	948	271	12.7	721	168	8.0	790	293	13.4	1042	339	16.1
May	768	232	11.2	712	203	9.7	695	248	11.8	1006	350	17.8
Jun	815	194	9.4	622	143	6.0	722	162	7.9	802	183	9.2
Jul	774	181	8.3	684	168	5.4	816	168	7.8	560	143	7.0
Aug	807	231	11.1	576	157	7.3	850	242	11.3	557	101	4.4
Sep	515	137	6.3	442	93	4.1	555	144	6.3	314	63	2.4
Oct	416	109	4.7	270	77	3.1	364	87	3.6	475	98	3.8
Nov	448	148	5.8	1	130	5.1	407	118	4.6	622	173	6.7
Annual Average												
Daily PAR ($\text{E m}^{-2} \text{ day}^{-1}$)		8.6			6.1				8.4			8.4
Annual Total												
PAR (E year^{-1})		3,138			2,240			3,061			3,071	

Table 11. Annual totals of PAR both in the water column and received by *Thalassia* (after epiphytic attenuation) at maximum depth limits in Tampa Bay.

	Water Column Annual PAR $E\ m^{-2}\ yr^{-1}$	Plant Available Annual PAR $E\ m^{-2}\ yr^{-1}$
MUL	4,864	3,138
PIN	3,639	2,240
PRT	4,876	3,061
RIV	4,934	3,071

Table 12. Seasonal and station means of epiphytic attenuation of PAR measured at stations in Sarasota Bay (n = 5 for each station-date).

DATE	Overall		Site 1		Site 2		Site 3		Site 4		Site 5		Site 6	
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
12/6/93	57.6	11.6	61.2	10.1	62.2	10.3	64.3	6.6	62.3	8.0	38.3	5.7	57.3	7.9
1/11/94	71.1	26.2	98.9	1.1	95.9	1.2	43.5	21.4	89.1	6.1	46.2	16.3	52.8	9.6
2/28/94	40.5	15.2	53.2	13.5	32.3	9.7	28.7	7.2	33.8	13.2	41.0	16.4	53.8	15.2
3/21/94	53.7	14.1	43.3	12.2	53.6	13.3	67.8	6.6	65.6	9.9	47.0	6.9	44.9	16.3
4/19/94	40.1	16.3	36.1	4.9	41.2	13.0	50.5	8.2	30.7	5.5	29.4	14.5	52.5	29.7
5/16/94	42.2	13.2	38.1	6.8	25.8	7.0	61.0	9.0	39.9	3.6	50.9	11.6	37.3	6.6
6/14/94	32.1	12.9	48.4	5.8	22.9	7.7	35.9	4.7	19.0	5.0	21.9	6.9	44.4	8.8
7/12/94	42.3	10.9	35.1	4.4	39.7	15.2	57.0	8.5	41.2	7.1	36.2	5.1	44.5	10.0
8/22/94	38.0	18.3	30.3	3.5	61.0	1.7	63.0	4.1	17.7	1.7	20.1	5.2	36.2	4.5
9/19/94	64.7	16.5	72.2	8.3	89.7	2.4	63.0	4.3	70.1	6.3	45.0	11.5	48.1	8.1
10/21/94	63.5	26.3	54.9	12.1	91.0	6.8	73.6	4.5	13.1	11.0	67.5	7.8	80.6	8.2
YEAR	49.6	21.2	52.0	20.5	55.9	26.7	55.3	15.6	43.9	24.6	40.3	16.1	50.2	16.5

Table 13. Mean percentage of PAR at target depths of 1.34 m, 1.84 m, 1.84 m, and 2.34 m for HB, respectively (1.0 m, 1.5 m, 1.5 m, 2.0 m MLLW). Annual water column requirement of 22.5% based on plant requirement of 13.8% annually, and mean epiphyte attenuation of 38.7% for the year. Final column assumes a calculated water column requirement of 27.5 % based on 13.8 % annual plant requirement and annual epiphytic attenuation of 50 %.

STATION	n	Percentage PAR at target water depths					Maximum water depth reached by			
		Maximum (%)	Minimum (%)	Mean (%)	s.d. (%)	k (m^{-1})	22.5% PAR WI (m)	38.7% Epi Attn (m)	Meets?	27.6% PAR w/ 50.0% Epi Attn (m)

Hillsborough Bay - Target = 1.34 m MSL (1.0 m MLLW)

HCEPC74	12	20.7	0.9	11.8	7.8	1.59	0.94	No	0.81	No
HCEPC44	12	30.8	0.1	12.3	7.8	1.56	0.95	No	0.82	No
COT17	28	60.9	1.4	15.3	14.5	1.40	1.07	No	0.92	No
HCEPC8	12	30.8	5.9	15.6	7.7	1.39	1.08	No	0.93	No
COT18	27	64.3	2.6	16.3	15.2	1.35	1.10	No	0.95	No
COT4	68	49.2	1.0	16.3	12.0	1.35	1.10	No	0.95	No
HCEPC71	12	41.3	9.3	17.3	10.6	1.31	1.14	No	0.98	No
HCEPC7	12	49.3	2.9	17.5	12.2	1.30	1.15	No	0.99	No
HCEPC70	12	36.3	9.3	18.0	9.1	1.28	1.17	No	1.01	No
HCEPC6	12	47.5	9.3	20.4	13.4	1.19	1.26	No	1.08	No
COT20	27	72.5	4.1	21.3	16.0	1.15	1.29	No	1.12	No
HCEPC73	12	43.5	2.9	22.2	13.4	1.12	1.33	No	1.15	No
COT19	28	73.5	6.1	23.1	16.2	1.09	1.37	Yes	1.18	No
HCEPC58	12	49.3	9.3	24.4	9.8	1.05	1.42	Yes	1.22	No
HCEPC55	12	60.3	9.3	25.5	15.7	1.02	1.46	Yes	1.26	No
HCEPC2	12	49.3	2.9	26.1	15.5	1.00	1.49	Yes	1.28	No
HCEPC54	12	52.5	9.3	26.7	12.3	0.98	1.52	Yes	1.31	No
HCEPC52	12	58.0	9.3	26.9	14.4	0.98	1.52	Yes	1.31	No
COT41	51	77.5	1.1	28.3	13.7	0.94	1.58	Yes	1.37	Yes
HCEPC80	12	52.5	13.3	29.4	14.4	0.91	1.63	Yes	1.41	Yes

Old Tampa Bay - Target = 1.84 m MSL (1.5 m MLLW)

HCEPC64	12	10.6	0.3	6.2	3.5	1.51	0.99	No	0.85	No
HCEPC62	12	22.4	2.7	12.0	6.1	1.15	1.29	No	1.11	No
HCEPC60	12	25.0	2.7	13.2	7.4	1.10	1.36	No	1.17	No
HCEPC65	12	27.6	2.7	16.3	8.9	0.99	1.51	No	1.30	No
HCEPC46	12	36.8	2.7	16.7	10.1	0.97	1.53	No	1.32	No
HCEPC66	12	36.8	2.7	17.6	10.8	0.95	1.58	No	1.36	No
HCEPC61	12	34.7	10.6	18.6	8.6	0.92	1.63	No	1.41	No
HCEPC67	12	36.8	7.7	20.1	10.2	0.87	1.71	No	1.47	No
HCEPC47	12	40.7	7.7	22.4	10.8	0.81	1.83	No	1.58	No
HCEPC38	12	36.8	7.7	22.8	10.0	0.80	1.86	Yes	1.60	No
COT40	3	50.6	11.2	24.6	22.5	0.76	1.96	Yes	1.69	No
HCEPC40	12	50.0	7.7	25.0	14.4	0.75	1.98	Yes	1.71	No
HCEPC36	12	48.7	10.6	28.7	13.8	0.68	2.20	Yes	1.90	Yes
HCEPC63	12	135.6	2.7	29.0	35.9	0.67	2.22	Yes	1.92	Yes
HCEPC68	12	48.7	13.5	29.2	11.9	0.67	2.23	Yes	1.93	Yes

Table 13. Continued.

STATION	n	Percentage PAR at target water depths					Maximum water depth reached by			
		Maximum (%)	Minimum (%)	Mean (%)	s.d. (%)	k (m^{-1})	22.5% PAR w/ 38.7% Epi Attn (m)	27.6% PAR w/ 50.0% Epi Attn (m)	Meets?	Meets?
HCEPC50	12	135.6	2.7	34.4	33.5	0.58	2.57	Yes	2.22	Yes
HCEPC41	12	135.6	10.6	35.3	33.2	0.57	2.64	Yes	2.28	Yes
HCEPC51	12	135.6	10.6	40.5	33.3	0.49	3.04	Yes	2.62	Yes
Middle Tampa Bay - Target = 1.85 m MSL (1.5 m MLLW)										
HCEPC84	12	15.7	1.2	7.2	4.7	1.43	1.04	No	0.90	No
HCEPC11	12	22.8	0.4	8.8	6.6	1.32	1.13	No	0.97	No
HCEPC9	12	38.1	2.4	13.6	11.3	1.08	1.38	No	1.19	No
COT12	12	42.1	4.5	16.5	11.1	0.98	1.52	No	1.31	No
HCEPC82	12	42.5	1.2	17.7	12.8	0.94	1.59	No	1.37	No
HCEPC81	12	45.3	6.2	21.2	12.8	0.84	1.77	No	1.53	No
HCEPC28	12	33.0	8.4	21.5	9.0	0.83	1.79	No	1.54	No
HCEPC13	12	42.5	2.4	21.9	13.7	0.83	1.81	No	1.56	No
HCEPC16	12	39.7	4.2	22.4	10.7	0.81	1.84	No	1.58	No
HCEPC32	12	47.7	6.2	23.4	13.2	0.79	1.89	Yes	1.63	No
HCEPC33	12	39.7	10.8	24.7	11.3	0.76	1.96	Yes	1.69	No
HCEPC19	12	42.5	10.8	27.6	12.1	0.70	2.13	Yes	1.84	Yes
HCEPC14	12	54.0	10.8	28.1	15.3	0.69	2.16	Yes	1.87	Yes
COT13	17	55.5	5.0	29.9	17.1	0.66	2.27	Yes	1.96	Yes
Lower Tampa Bay - Target = 2.34 m MSL (2.0 m MLLW)										
HCEPC25	12	18.9	4.4	10.0	4.5	0.98	1.52	No		
HCEPC96	12	20.9	4.4	11.3	6.5	0.93	1.60	No		
HCEPC24	12	35.3	4.4	16.3	8.9	0.78	1.92	No		
HCEPC21	12	38.2	6.2	19.3	11.2	0.70	2.12	No		
HCEPC90	12	35.3	10.3	20.2	7.8	0.68	2.18	No		
HCEPC91	12	40.9	14.6	24.3	8.7	0.60	2.47	Yes		
HCEPC94	12	48.9	4.4	25.2	13.8	0.59	2.53	Yes		
HCEPC95	12	45.8	8.1	25.4	11.3	0.59	2.55	Yes		
HCEPC92	12	35.3	12.4	25.5	7.0	0.58	2.55	Yes		
HCEPC93	11	43.4	16.7	27.0	10.7	0.56	2.66	Yes		
HCEPC23	12	40.9	10.3	28.3	11.2	0.54	2.77	Yes		
COT95	7	62.6	16.1	40.6	18.3	0.39	3.87	Yes		

Table 14. Mean percentage of PAR at target depths of 1.34 m, 1.84 m, 1.84 m, and 2.34 m for HB respectively (1.0 m, 1.5 m, 1.5 m, 2.0 m MLLW). Water column requirement during the growing season 16.1% based on plant requirement of 12.0% and mean seasonal epiphyte attenuation of 25.5 %. Final column assumes a calculated water column requirement of 21.4 % based on 12.0 % seasonal plant requirement and growing season epiphytic attenuation of 43.9 %.

STATION	n	Percentage PAR at target water depths					Maximum water depth reached by			
		Maximum (%)	Minimum (%)	Mean (%)	s.d. (%)	k (m^{-1})	16.1% PAR w/ 25.5% Epi Attn (m)	21.4% PAR w/ 43.9% Epi Attn (m)	Meets?	Meets?
Hillsborough Bay - Target = 1.34 m MSL (1.0 m MLLW)										
HCEPC74	5	17.1	0.9	5.34	6.63	2.19	0.84	No	0.71	No
COT17	11	14.3	1.4	8.14	3.78	1.87	0.98	No	0.82	No
HCEPC44	5	13.3	5.9	10.22	3.14	1.70	1.07	No	0.91	No
COT18	11	19.0	2.6	10.68	5.14	1.67	1.09	No	0.92	No
HCEPC71	5	17.1	9.3	11.66	3.5	1.60	1.14	No	0.96	No
HCEPC8	5	17.1	5.9	11.74	5.09	1.60	1.14	No	0.96	No
HCEPC73	5	24.2	2.9	11.88	8.69	1.59	1.15	No	0.97	No
COT20	11	30.3	4.2	12.09	7.83	1.58	1.16	No	0.98	No
COT4	30	29.1	1.0	12.45	7.55	1.55	1.17	No	0.99	No
HCEPC7	5	17.1	2.9	12.74	5.82	1.54	1.19	No	1.00	No
HCEPC6	5	17.1	9.3	14.02	3.25	1.47	1.25	No	1.05	No
COT19	11	23.8	6.2	14.43	6.07	1.44	1.26	No	1.07	No
HCEPC55	5	20.7	9.3	14.7	5.14	1.43	1.28	No	1.08	No
HCEPC70	5	17.1	13.3	15.58	2.08	1.39	1.32	No	1.11	No
HCEPC80	5	36.3	13.3	20.08	10.22	1.20	1.52	Yes	1.29	No
HCEPC2	5	39.8	9.3	20.64	13.1	1.18	1.55	Yes	1.31	No
HCEPC52	5	27.7	17.1	20.64	5.0	1.18	1.55	Yes	1.31	No
HCEPC58	5	30.8	17.1	22.68	5.76	1.11	1.65	Yes	1.39	Yes
HCEPC54	5	43.5	9.3	22.96	12.74	1.10	1.66	Yes	1.40	Yes
COT41	21	49.2	1.1	24.32	10.92	1.06	1.73	Yes	1.46	Yes
Old Tampa Bay - Target = 1.84 m MSL (1.5 m MLLW)										
HCEPC64	5	10.6	0.3	6.26	4.38	1.51	1.21	No	1.02	No
HCEPC62	5	13.5	2.7	8.46	4.48	1.34	1.36	No	1.15	No
HCEPC66	5	13.5	2.7	9.02	4.57	1.31	1.40	No	1.18	No
HCEPC65	5	19.6	2.7	9.24	7.3	1.29	1.41	No	1.19	No
HCEPC63	5	13.5	2.7	9.62	5.37	1.27	1.44	No	1.21	No
HCEPC46	5	16.5	2.7	9.64	5.78	1.27	1.44	No	1.21	No
HCEPC60	5	22.4	2.7	10.98	8.63	1.20	1.52	No	1.28	No
COT40	2	12.1	11.2	11.65	0.64	1.17	1.56	No	1.32	No
HCEPC61	5	13.5	10.6	12.34	1.59	1.14	1.61	No	1.36	No
HCEPC47	5	27.6	7.7	15.78	7.63	1.00	1.82	No	1.54	No
HCEPC67	5	34.7	7.7	16.6	10.64	0.98	1.87	Yes	1.58	No
HCEPC40	5	27.6	7.7	18.06	8.21	0.93	1.96	Yes	1.66	No
HCEPC41	5	25.0	10.6	19.9	6.25	0.88	2.08	Yes	1.76	No
HCEPC38	5	34.7	13.5	20.72	8.46	0.86	2.13	Yes	1.80	No

Table 14. Continued.

STATION	n	Percentage PAR at target water depths					Maximum water depth reached by			
		Maximum (%)	Minimum (%)	Mean (%)	s.d. (%)	k (m ⁻¹)	16.1% PAR w/ 25.5% Epi Attn (m)	Meets?	21.4% PAR w/ 43.9% Epi Attn (m)	Meets?
HCEPC50	5	34.7	2.7	21.82	12.65	0.83	2.21	Yes	1.86	Yes
HCEPC36	5	38.9	10.6	25.74	11.76	0.74	2.48	Yes	2.09	Yes
HCEPC68	5	36.8	16.5	26.18	7.72	0.73	2.51	Yes	2.12	Yes
HCEPC51	5	40.7	10.6	28.28	13.78.	0.69	2.66	Yes	2.25	Yes
Middle Tampa Bay - Target = 1.85 m (MSL) (1.5 m MLLW)										
HCEPC11	5	6.2	0.4	3.88	2.51	1.77	1.03	No	0.87	No
HCEPC84	5	10.8	1.2	4.96	3.77	1.63	1.12	No	0.94	No
HCEPC9	5	10.8	2.4	6.48	3.85	1.49	1.23	No	1.04	No
COT12	5	28.6	4.5	11.58	9.69	1.17	1.56	No	1.32	No
HCEPC82	5	25	1.2	11.84	10.37	1.16	1.57	No	1.33	No
HCEPC13	5	25	2.4	13.4	9.17	1.09	1.67	No	1.41	No
HCEPC81	5	18.1	8.4	13.74	4	1.08	1.69	No	1.43	No
HCEPC32	5	29.1	6.2	18.78	9.79	0.91	2.01	Yes	1.70	No
HCEPC28	5	31.1	8.4	19.18	9.42	0.90	2.04	Yes	1.72	No
HCEPC14	5	29.1	13.3	19.32	6.08	0.89	2.04	Yes	1.73	No
HCEPC16	5	33	4.2	19.5	12.09	0.89	2.06	Yes	1.74	No
HCEPC33	5	33	10.8	22.24	9.76	0.82	2.24	Yes	1.89	Yes
COT13	8	49.7	5	22.57	15.98	0.81	2.26	Yes	1.91	Yes
HCEPC19	5	42.5	10.8	28.76	12.08	0.68	2.70	Yes	2.28	Yes
Lower Tampa Bay - Target = 2.34 m MSL (2.0 m MLLW)										
HCEPC25	5	18.9	4.4	10.38	5.54	0.97	1.89	No		
HCEPC96	5	20.9	4.4	10.52	7.74	0.96	1.90	No		
HCEPC24	5	28.6	8.1	14.78	8.51	0.82	2.24	No		
HCEPC21	5	28.6	8.1	16.08	7.98	0.78	2.34	No		
HCEPC90	5	28.6	12.4	18.24	6.27	0.73	2.51	Yes		
COT95	3	28.9	16.1	22.63	6.4	0.63	2.88	Yes		
HCEPC92	5	30.4	20.9	24.4	3.64	0.60	3.03	Yes		
HCEPC23	5	40.9	10.3	26.3	13.27	0.57	3.20	Yes		
HCEPC91	5	40.9	18.9	26.84	8.7	0.56	3.25	Yes		
HCEPC94	5	42.2	4.4	27.16	13.89	0.56	3.28	Yes		
HCEPC93	5	43.4	16.7	28.36	12.22	0.54	3.39	Yes		
HCEPC95	5	43.4	18.9	30.6	9.24	0.51	3.61	Yes		

Table 15. Plastochrone interval (days) and approximate numbers of blades produced per *Thalassia* shoot per year in Tampa Bay.

Sampling Date	MUL		PIN		PRT		RIV	
	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep
<u>Plastochrone Interval</u>								
Dec	999999	999999	999999	999999	224.0	240.0	999999	999999
Feb	70.0	52.5	105.0	105.0	91.0	31.5	105.0	75.0
Apr	17.5	21.0	8.8	105.0	17.5	30.0	13.1	13.1
Jun	999999	52.5	105.0	60.0	105.0	24.0	21.0	26.3
Aug	60.0	60.0	40.0	60.0	60.0	60.0	45.0	90.0
Oct	36.0	30.0	60.0	17.5	65.0	39.0	45.0	39.0
<u>Blades formed per 60 Days</u>								
Dec	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0
Feb	0.9	1.1	0.6	0.6	0.7	1.9	0.6	0.8
Apr	3.4	2.9	6.9	0.6	3.4	2.0	4.6	4.6
Jun	0.0	1.1	0.6	1.0	0.6	2.5	2.9	2.3
Aug	1.0	1.0	1.5	1.0	1.0	1.0	1.3	0.7
Oct	1.7	2.0	1.0	3.4	0.9	1.5	1.3	1.5
Blades per Year	7	8	11	7	7	9	11	10

999999 - no new shoots observed

Table 16. Photosynthesis/ix-radiance parameters determined on *Thalassia* leaf segments from Tampa Bay during April and June. Units are α ($\mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1}$) $\mu\text{E m}^{-2} \text{ sec}^{-1}$); I_c and I_k , $\mu\text{E m}^{-2} \text{ sec}^{-1}$; P_{\max} , $\mu\text{g O}_2 \text{ gdwt}^{-1} \text{ min}^{-1}$; chlorophyll a and b, mg gdwt $^{-1}$. (Data from Dr. C.J. Dawes)

Station	Parameter	April		June	
		Mean	s.d.	Mean	s.d.
MUL-S	α	0.150	0.000	1.333	0.494
MUL-D	α	0.233	0.103	0.350	0.071
MUL-S	I_c	89	6	24	6
MUL-D	I_c	93	19	10	0
MUL-S	I_k	251	13	117	59
MUL-D	I_k	180	0	200	0
MUL-S	P_{\max}	35.8	3.8	164.0	106.1
MUL-D	P_{\max}	41.3	17.9	73.7	14.3
MUL-S	Chl <i>a</i>	1.3	0.1	2.5	0.4
MUL-D	Chl <i>a</i>	1.3	0.2	2.6	1
MUL-S	Chl <i>b</i>	0.9	0.1	1.9	0.2
MUL-D	Chl <i>b</i>	0.7	0.2	2	0.7
PIN-S	α	0.200	0.041	0.900	0.122
PIN-D	α	0.217	0.024	0.500	0.082
PIN-S	I_c	64	10	10	0
PIN-D	I_c	75	3	15	4
PIN-S	I_k	183	1	167	25
PIN-D	I_k	225	17	192	19
PIN-S	P_{\max}	34.8	7.6	148.0	24.1
PIN-D	P_{\max}	49.7	4.4	113.2	42.6
PIN-S	Chl <i>a</i>	1.1	0.3	2.7	0.6
PIN-D	Chl <i>a</i>	1.1	0.3	4.1	0.6
PIN-S	Chl <i>b</i>	0.8	0.2	2.1	0.4
PIN-D	Chl <i>b</i>	0.8	0.2	3.1	0.4
PRT-S	α	0.333	0.024	2.850	1.059
PRT-D	α	0.200	0.000	1.650	0.878
PRT-S	I_c	57	11	13	2
PRT-D	I_c	70	1	13	5
PRT-S	I_k	283	18	110	49
PRT-D	I_k	287	27	98	18
PRT-S	P_{\max}	88.7	11.2	277.2	67.0
PRT-D	P_{\max}	58.8	5.8	178.0	117.1
PRT-S	Chl <i>a</i>	2.2	0.2	3.2	0.4

Table 16. Continued.

Page 2

Station	Parameter	April		June	
		Mean	s.d.	Mean	s.d.
PRT-D	Chl <i>a</i>	1.3	0.3	2.6	0.6
PRT-S	Chl <i>b</i>	0.6	0.2	2.4	0.2
PRT-D	Chl <i>b</i>	0.9	0.2	2	0.4
RIV-S	α	1.017	1.049	1.167	0.165
RIV-D	α	0.167	0.047	0.933	0.249
RIV-S	I_c	48	9	15	4
RIV-D	I_c	76	25	13	5
RIV-S	I_k	208	37	138	26
RIV-D	I_k	202	28	183	24
RIV-S	P_{max}	57.3	11.1	157.0	9.9
RIV-D	P_{max}	36.0	5.7	186.7	47.1
RIV-S	Chl <i>a</i>	1.4	0.2	4.1	0.4
RIV-D	Chl <i>a</i>	1.2	0.2	3	0.3
RIV-S	Chl <i>b</i>	0.9	0.2	3.2	0.2
RIV-D	Chl <i>b</i>	0.7	0.3	2.2	0.2

Appendix A

Seagrass Restoration Targets for Tampa Bay

SEAGRASS RESTORATION AND PROTECTION AREAS

Old Tampa Bay

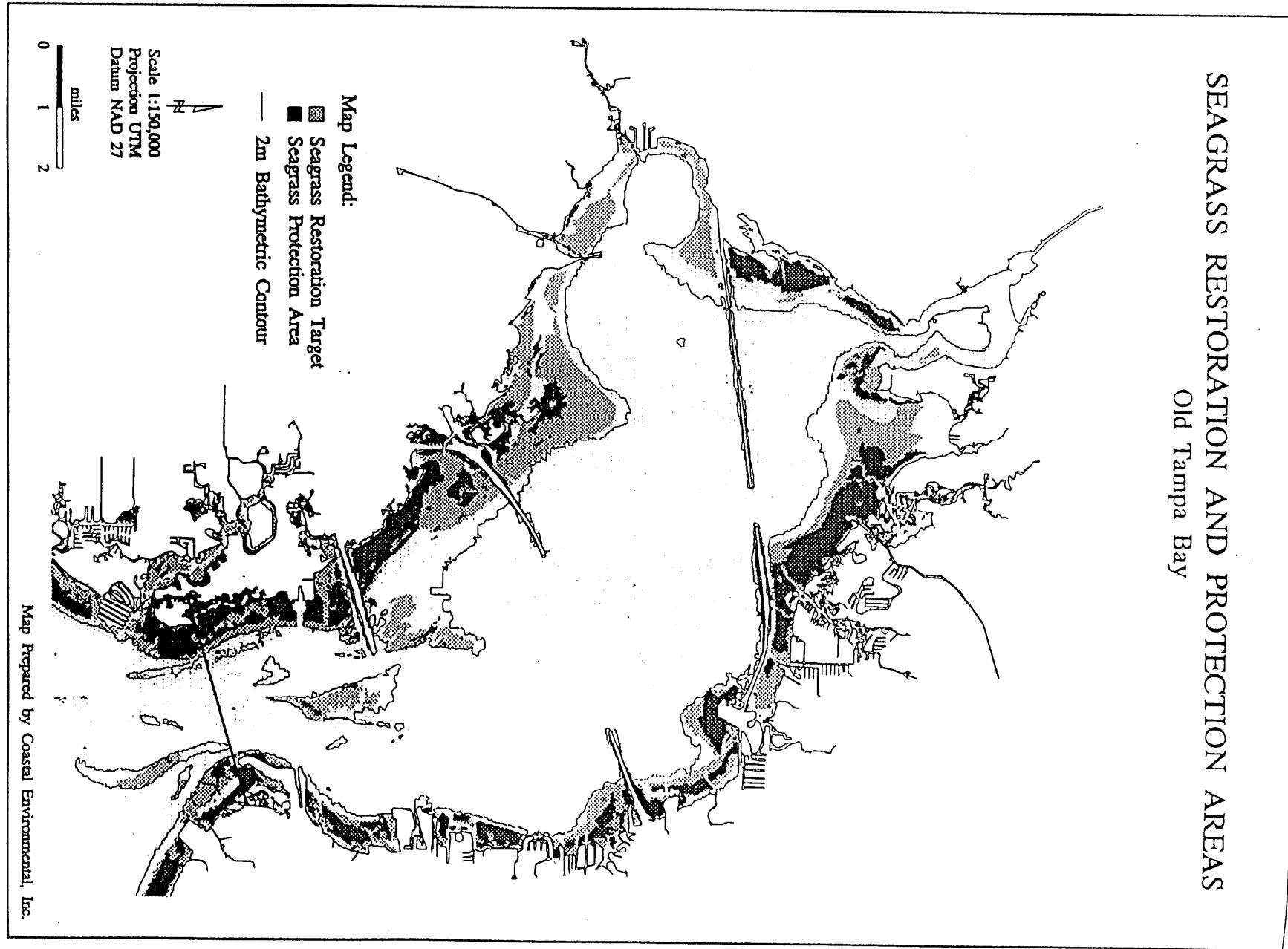


Figure 4.20 Seagrass restoration and protection targets in Old Tampa Bay.

SEAGRASS RESTORATION AND PROTECTION AREAS Hillsborough Bay

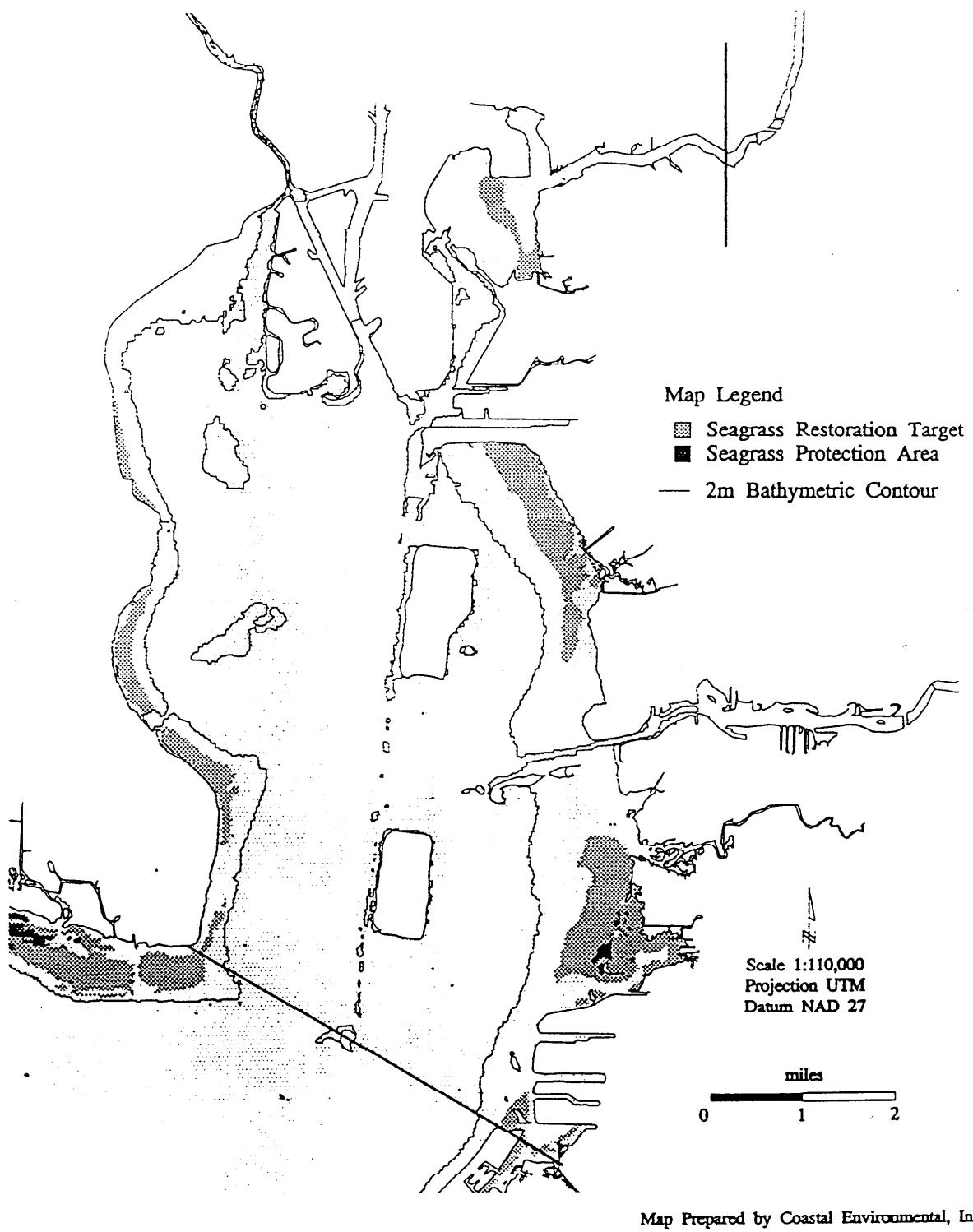


Figure 4.21

Seagrass restoration and protection targets in Hillsborough Bay.

SEAGRASS RESTORATION AND PROTECTION AREAS Middle Tampa Bay

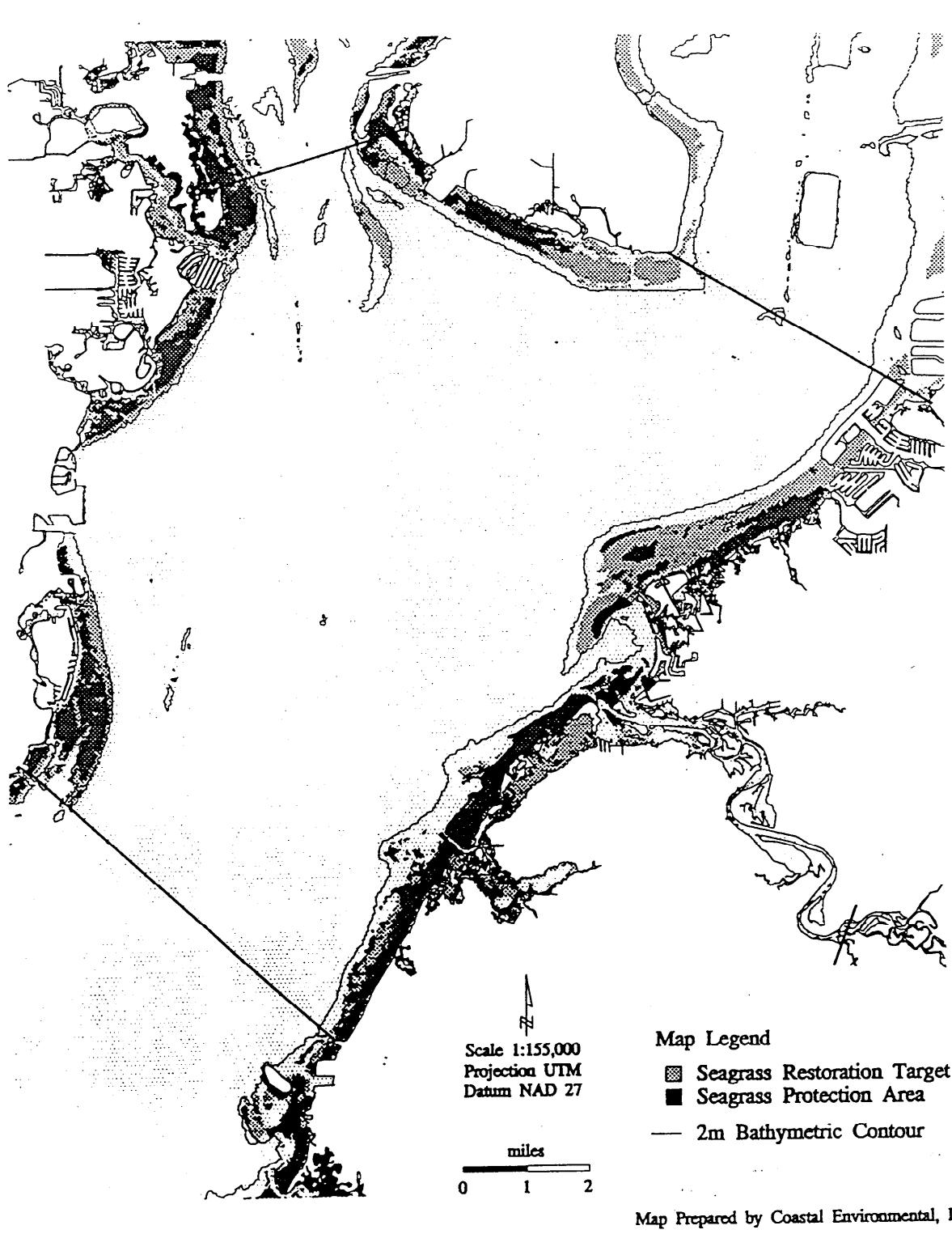


Figure 4.22

Seagrass restoration and protection targets in Middle Tampa Bay.

SEAGRASS RESTORATION AND PROTECTION AREAS Lower Tampa Bay

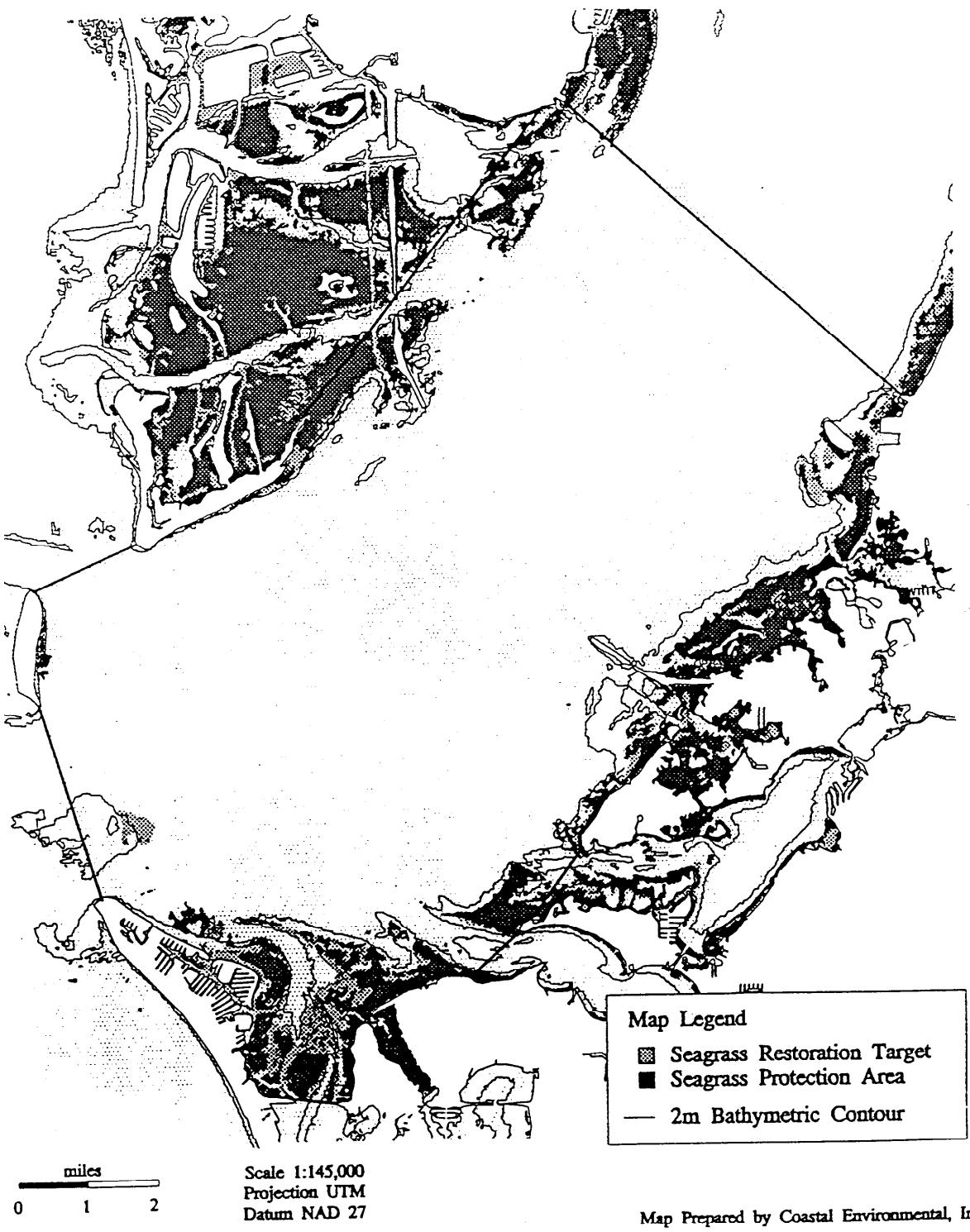


Figure 4.23

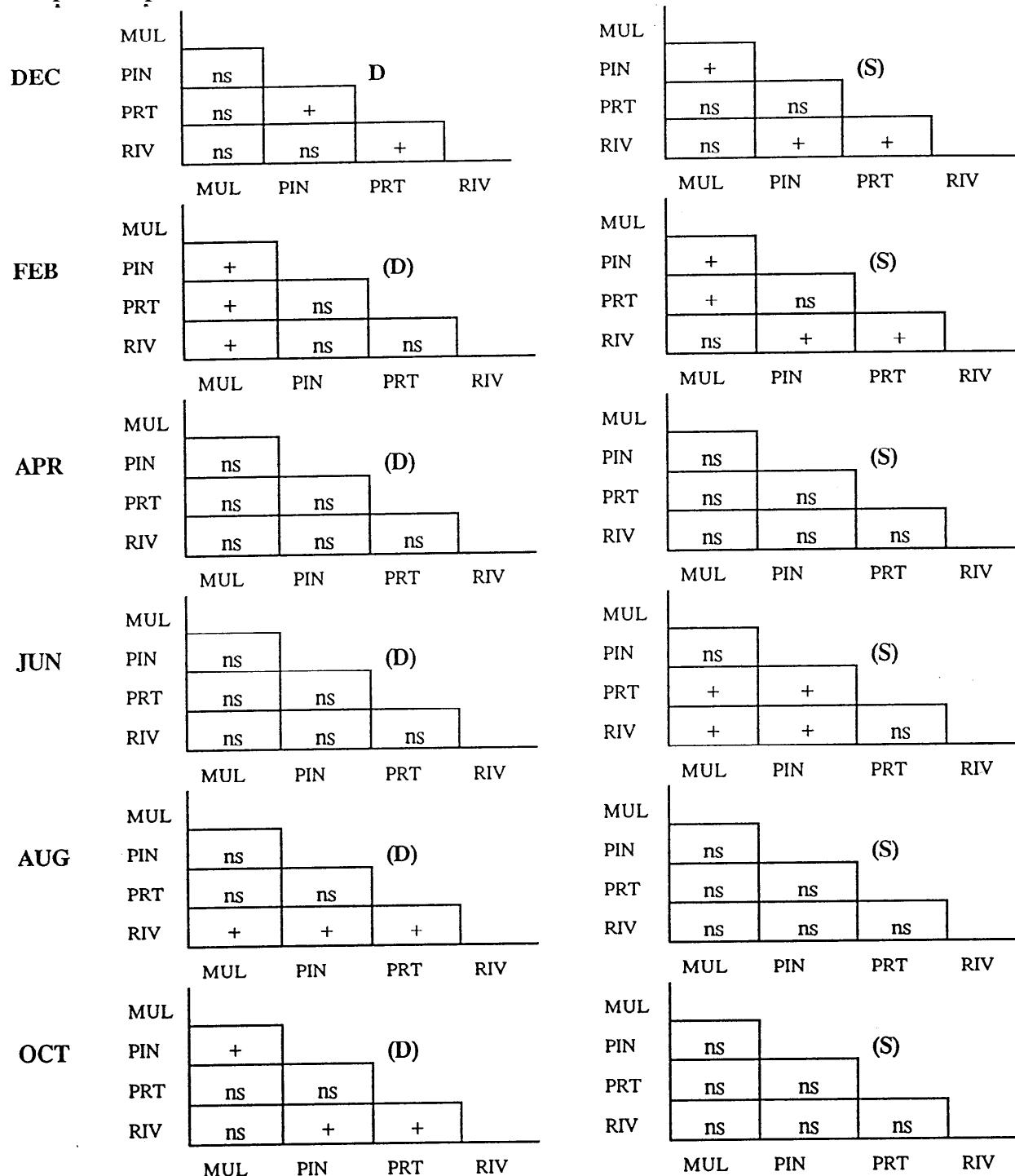
Seagrass restoration and protection targets in Lower Tampa Bay.

Appendix B

Statistical Results

Appendix Table B. 1. Multiple comparison analyses and t-tests for ABOVE GROUND BIOMASS.

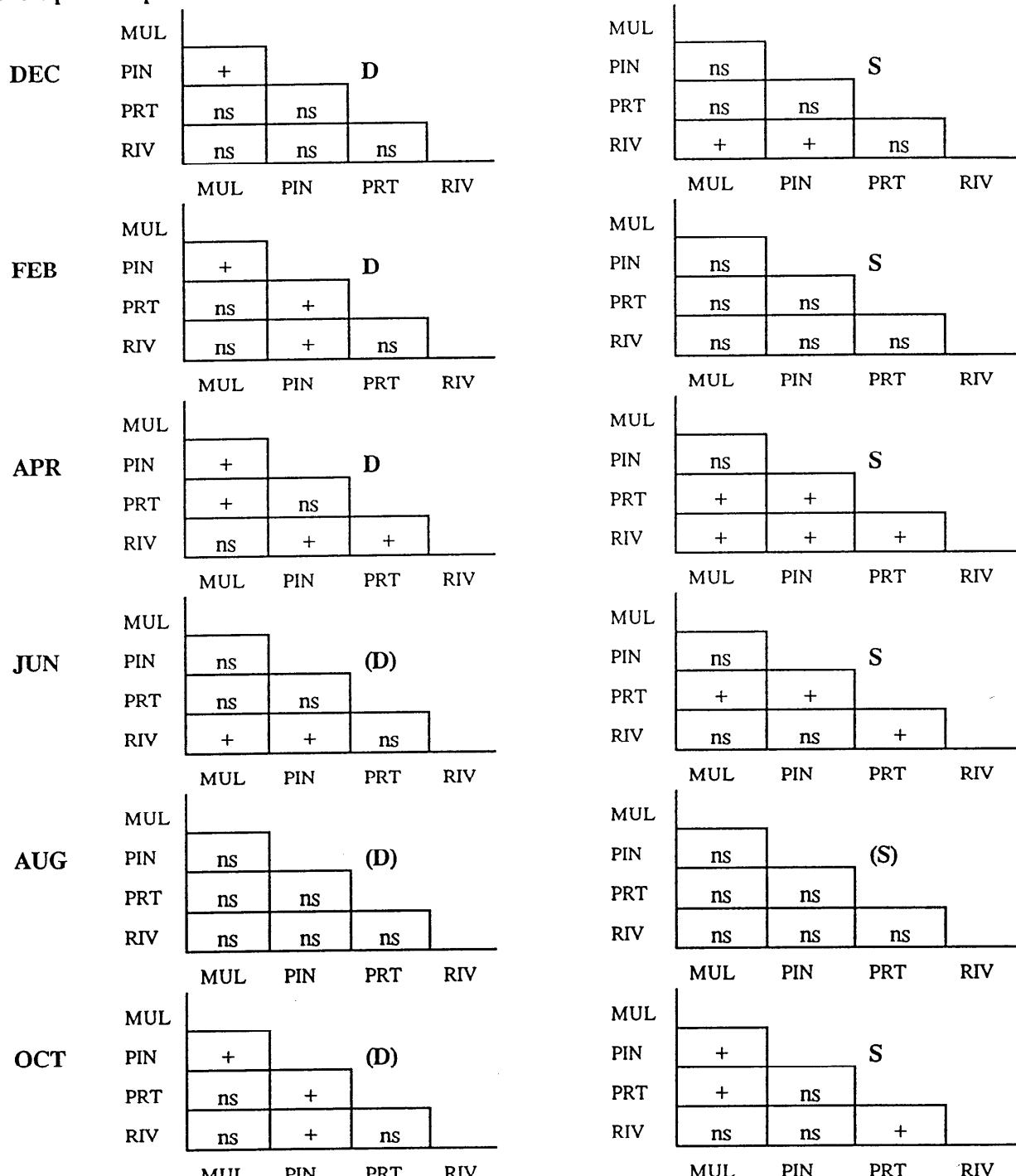
Multiple Comparison



		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	(+++)	(+++)	(+++)	(++)	(+++)	(+++)
PIN	S/D	+++	(+++)	(+++)	++	ns	+++
PRT	S/D	(+++)	(++)	(+++)	(++)	(+++)	(+++)
RIV	S/D	+++	(+++)	(+++)	(+++)	(+++)	(+++)

Appendix Table B.2. Multiple comparison analyses and t-tests for MEAN BLADE LENGTH PER SHOOT.

Multiple Comparison

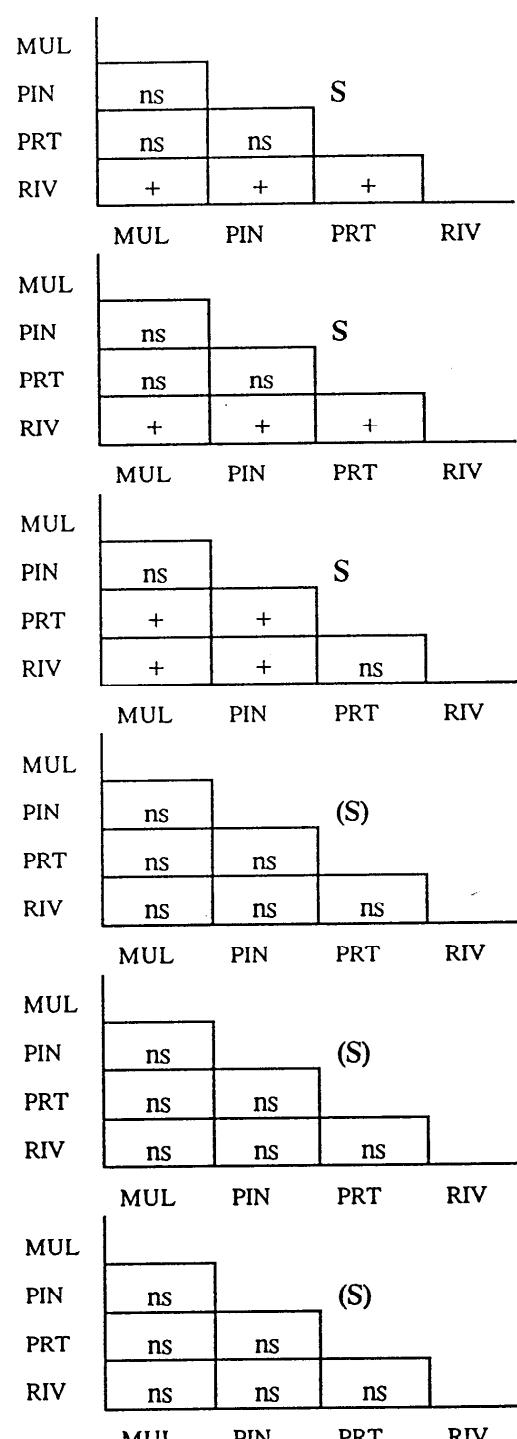
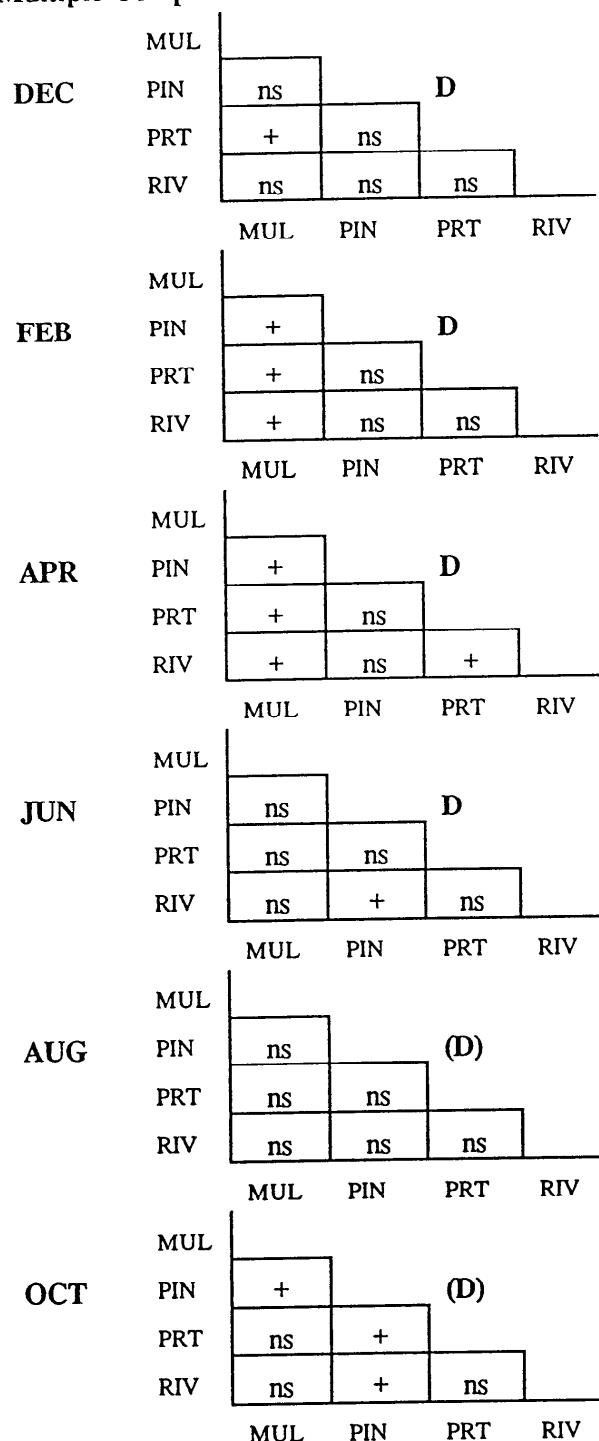


t-test

		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	+	+	ns	ns	ns	ns
PIN	S/D	(ns)	(ns)	+++	ns	(+++)	+++
PRT	S/D	ns	(ns)	ns	(+++)	+++	++
RIV	S/D	++	+++	+++	+++	++	(ns)

Appendix Table B-3. Multiple comparison analyses and t-tests for LEAF AREA PER SHOOT.

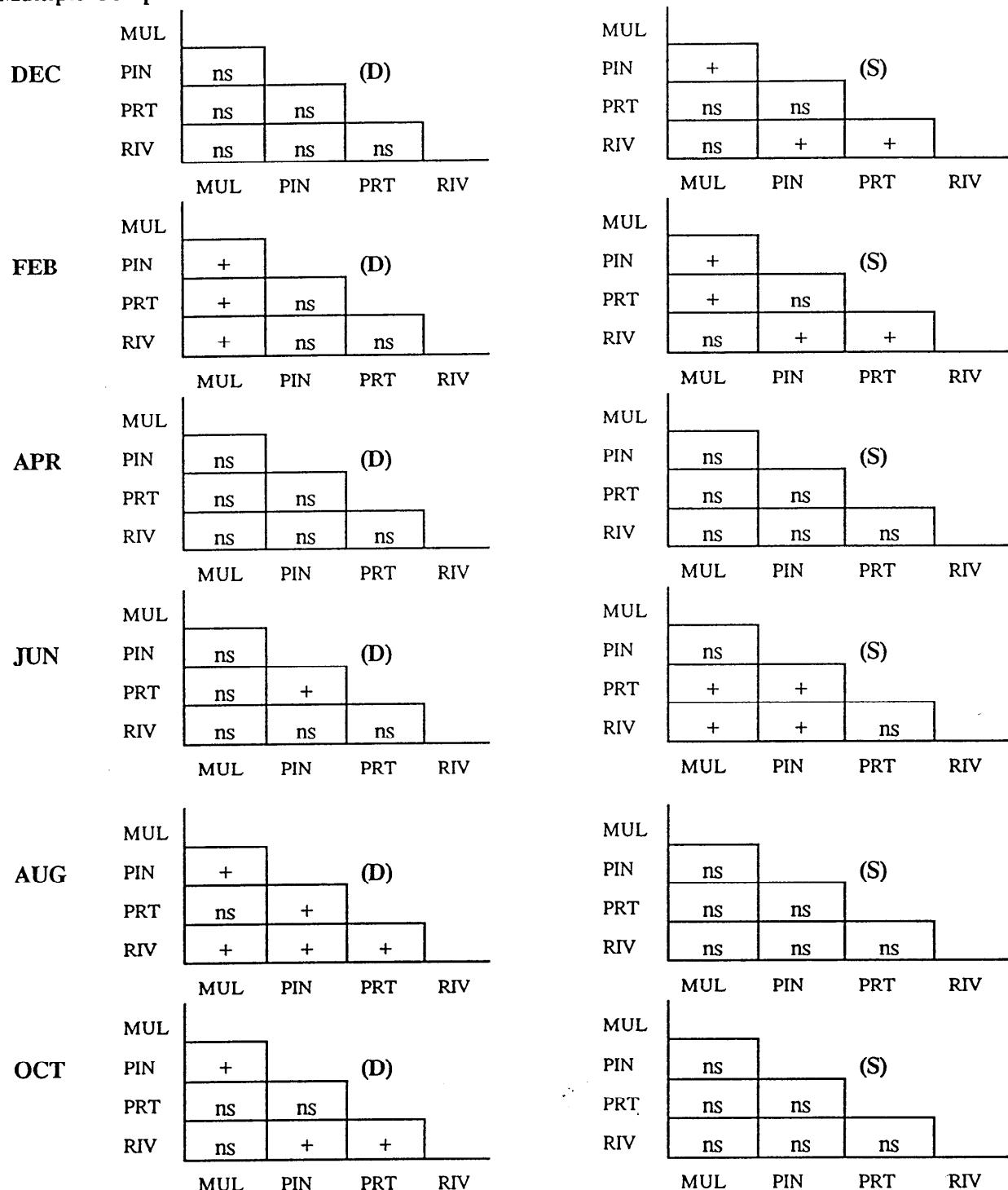
Multiple Comparison



t-test		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	+++	+++	++	ns	ns	ns
PIN	S/D	+	ns	ns	ns	++	(+)
PRT	S/D	ns	ns	ns	+	++	+
RIV	S/D	+++	+++	++	+++	+++	(++)

Appendix Table B.4. Multiple comparison analyses and t-tests for LEAF AREA INDEX.

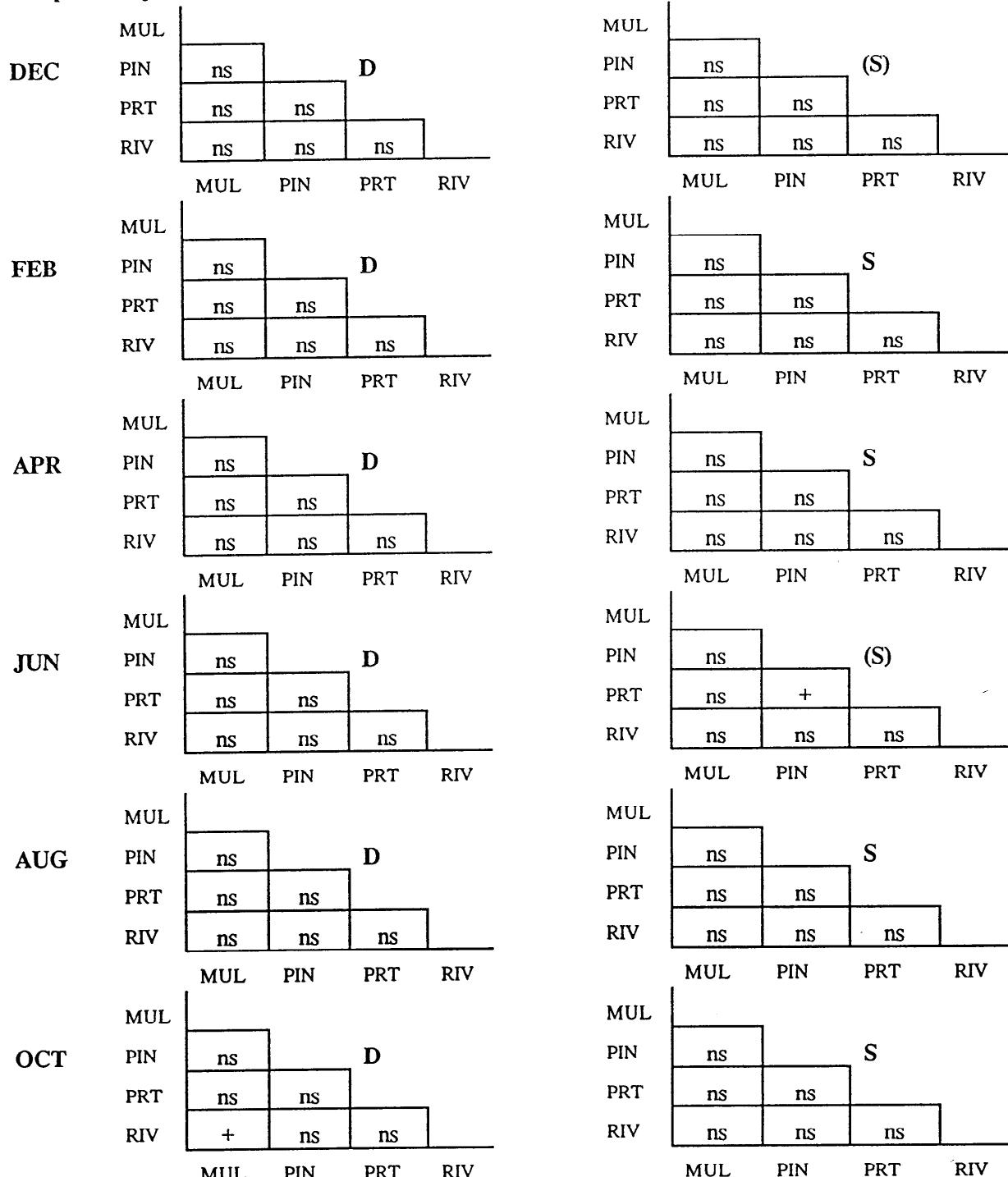
Multiple Comparison



t-test		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	(+++)	(+++)	(+++)	(++)	(+++)	(+++)
PIN	S/D	(+++)	(+++)	(+++)	+++	ns	+++
PRT	S/D	(+++)	(+++)	(+++)	(+++)	(+++)	(+++)
RIV	S/D	(+++)	(+++)	(+++)	(+++)	(+++)	(+++)

Appendix Table B.S. Multiple comparison analyses and t-tests for SOLUBLE RHIZOME CARBOHYDRATES.

Multiple Comparison



t-test

		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	ns	ns	ns	ns	ns	+++
PIN	S/D	(+++)	ns	+	(+++)	+++	++
PRT	S/D	+	+++	++	ns	(+++)	ns
RIV	S/D	ns	ns	ns	++	ns	ns

Appendix Table B.6. Multiple comparison analyses and t-tests for AREAL GROWTH.

Multiple Comparison

	MUL	PIN	PRT	RIV
DEC	ns		(D)	
	MUL	PIN	PRT	RIV
PRT	ns	ns		
RIV	ns	ns	ns	

	MUL	PIN	PRT	RIV
FEB	ns		(D)	
	MUL	PIN	PRT	RIV
PRT	+	+		
RIV	+	+	ns	

	MUL	PIN	PRT	RIV
APR	ns		(D)	
	MUL	PIN	PRT	RIV
PRT	ns	ns		
RIV	ns	ns	ns	

	MUL	PIN	PRT	RIV
JUN	ns		(D)	
	MUL	PIN	PRT	RIV
PRT	ns	ns		
RIV	ns	ns	ns	

	MUL	PIN	PRT	RIV
AUG	ns		(D)	
	MUL	PIN	PRT	RIV
PRT	ns	ns		
RIV	ns	ns	ns	

	MUL	PIN	PRT	RIV
OCT	+		(D)	
	MUL	PIN	PRT	RIV
PRT	ns	ns		
RIV	ns	+	ns	

	MUL	PIN	PRT	RIV
	ns		(S)	
	MUL	PIN	PRT	RIV
PRT	ns	ns		
RIV	ns	ns	ns	

	MUL	PIN	PRT	RIV
	ns		S	
	MUL	PIN	PRT	RIV
PRT	+	ns		
RIV	+	+	+	

	MUL	PIN	PRT	RIV
	ns		(S)	
	MUL	PIN	PRT	RIV
PRT	ns	ns		
RIV	ns	ns	ns	

	MUL	PIN	PRT	RIV
	ns		(S)	
	MUL	PIN	PRT	RIV
PRT	ns	ns		
RIV	+	+	+	

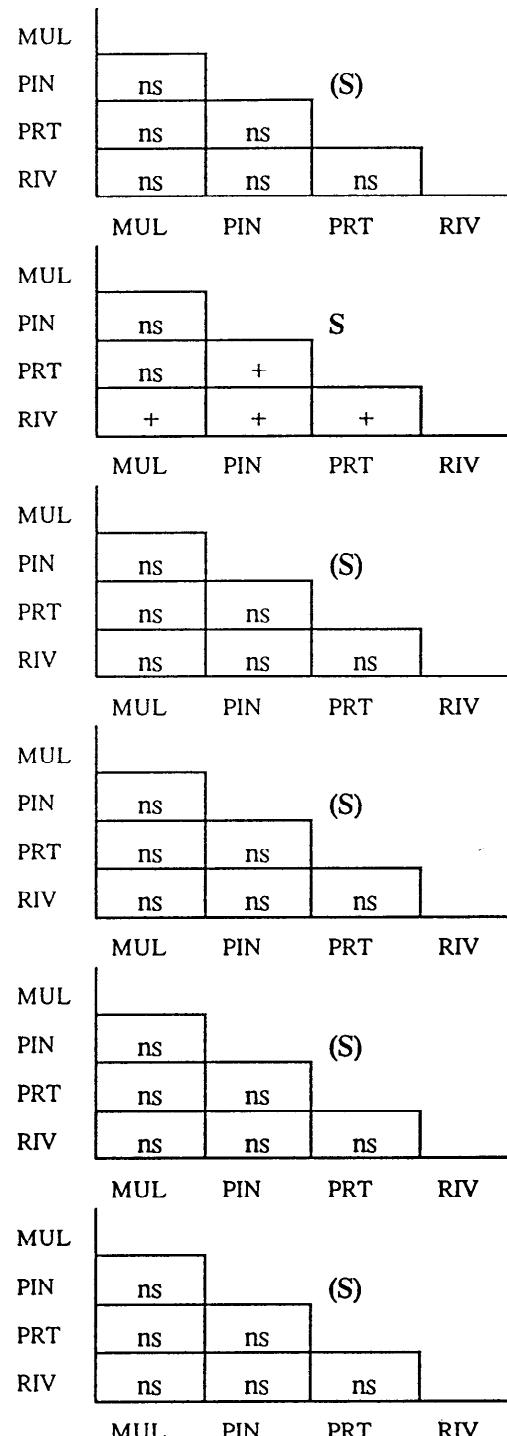
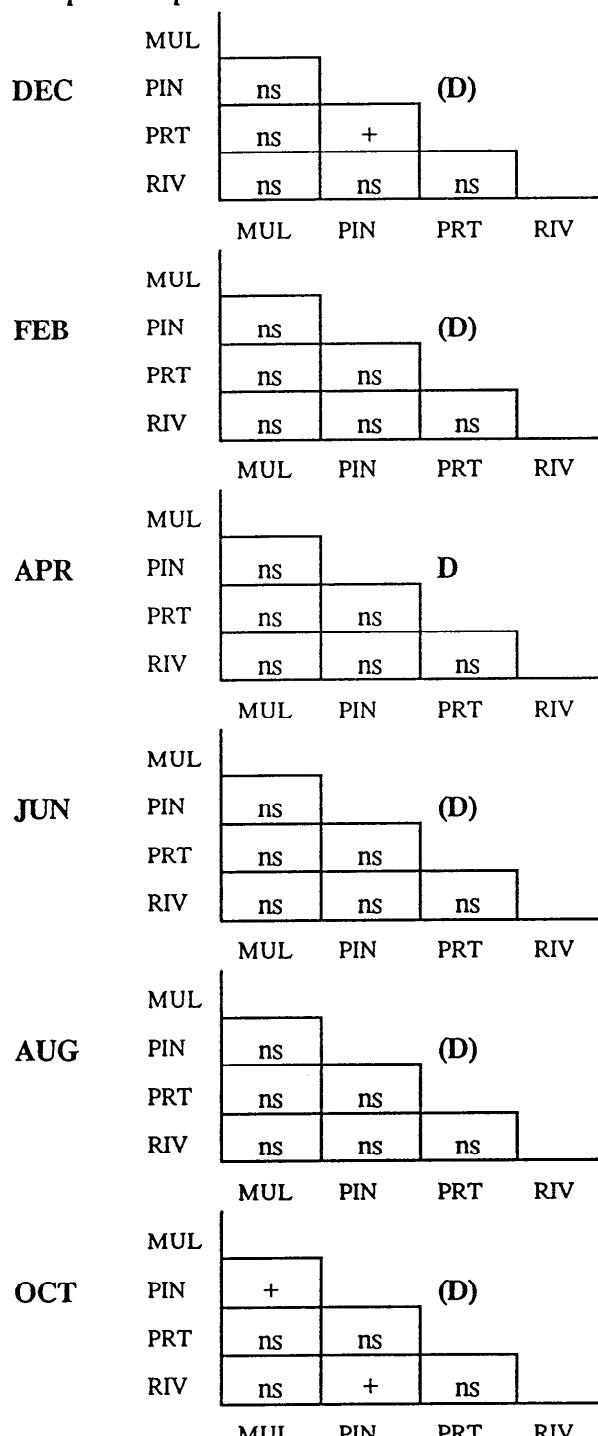
	MUL	PIN	PRT	RIV
	ns		(S)	
	MUL	PIN	PRT	RIV
PRT	ns	ns		
RIV	ns	ns	ns	

	MUL	PIN	PRT	RIV
	ns		(S)	
	MUL	PIN	PRT	RIV
PRT	ns	ns		
RIV	ns	ns	ns	

t-test		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	(+)	(+++)	(+++)	(+)	(+++)	(+++)
PIN	S/D	(++)	(+++)	(+++)	ns	ns	(+++)
PRT	S/D	(ns)	(ns)	(+++)	(++)	(+)	(++)
RIV	S/D	ns	(+++)	(+++)	(+++)	(+++)	(++)

Appendix Table B.7. Multiple comparison analyses and t-tests for ABOVE-GROUND GROWTH PER SHOOT.

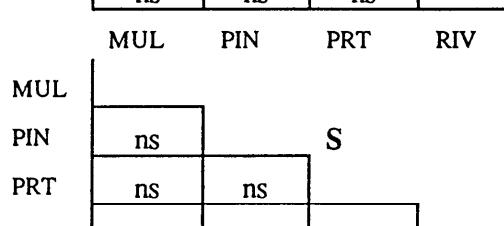
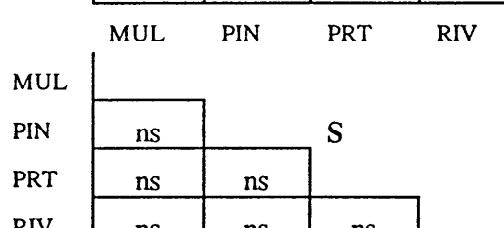
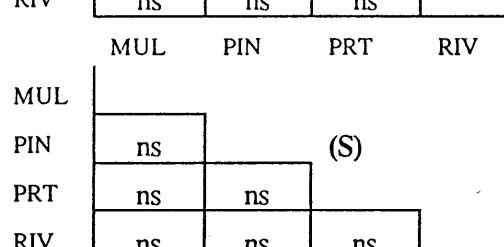
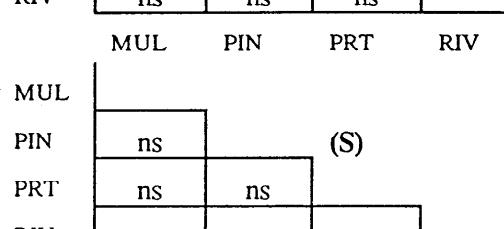
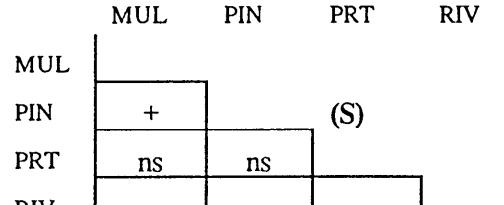
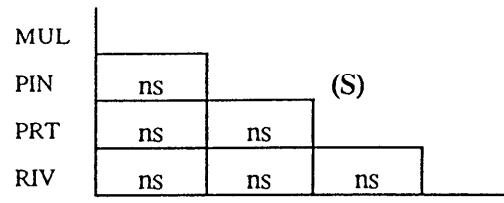
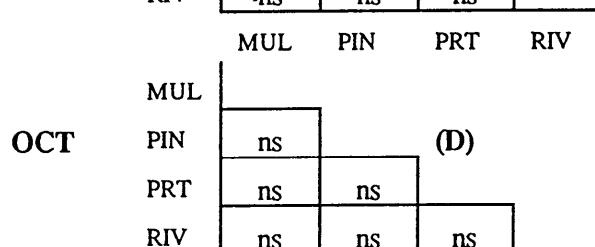
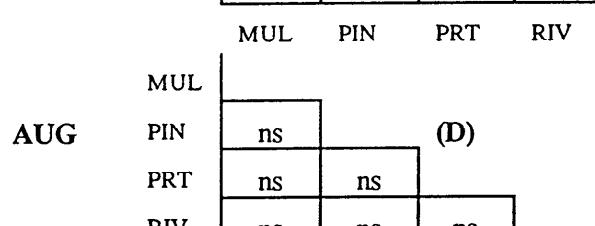
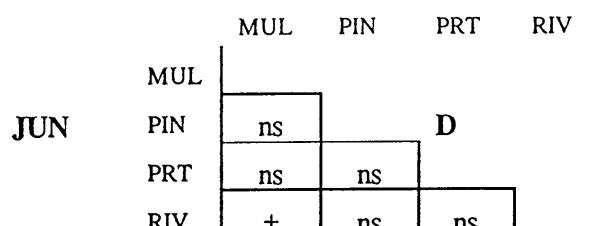
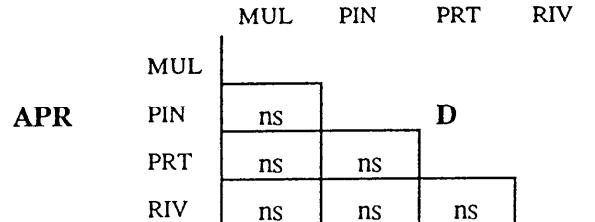
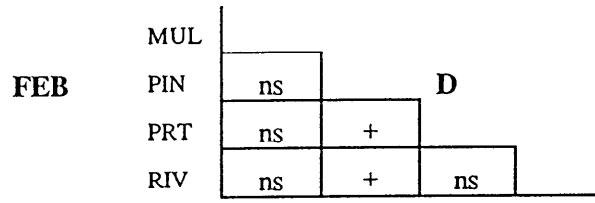
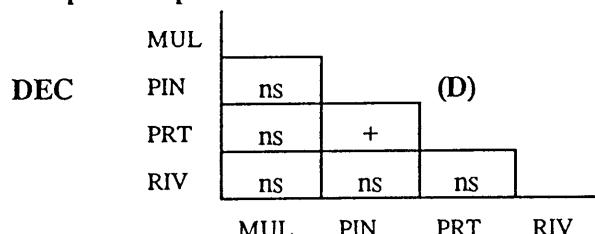
Multiple Comparison



t-test		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	ns	++	ns	ns	ns	(+++)
PIN	S/D	(+++)	++	(+++)	ns	ns	ns
PRT	S/D	(+++)	ns	++	(+++)	ns	(+++)
RIV	S/D	ns	+++	(+++)	+++	(+++)	(+++)

Appendix Table B.8. Multiple comparison analyses and t-tests for LEAF RELATIVE GROWTH RATE.

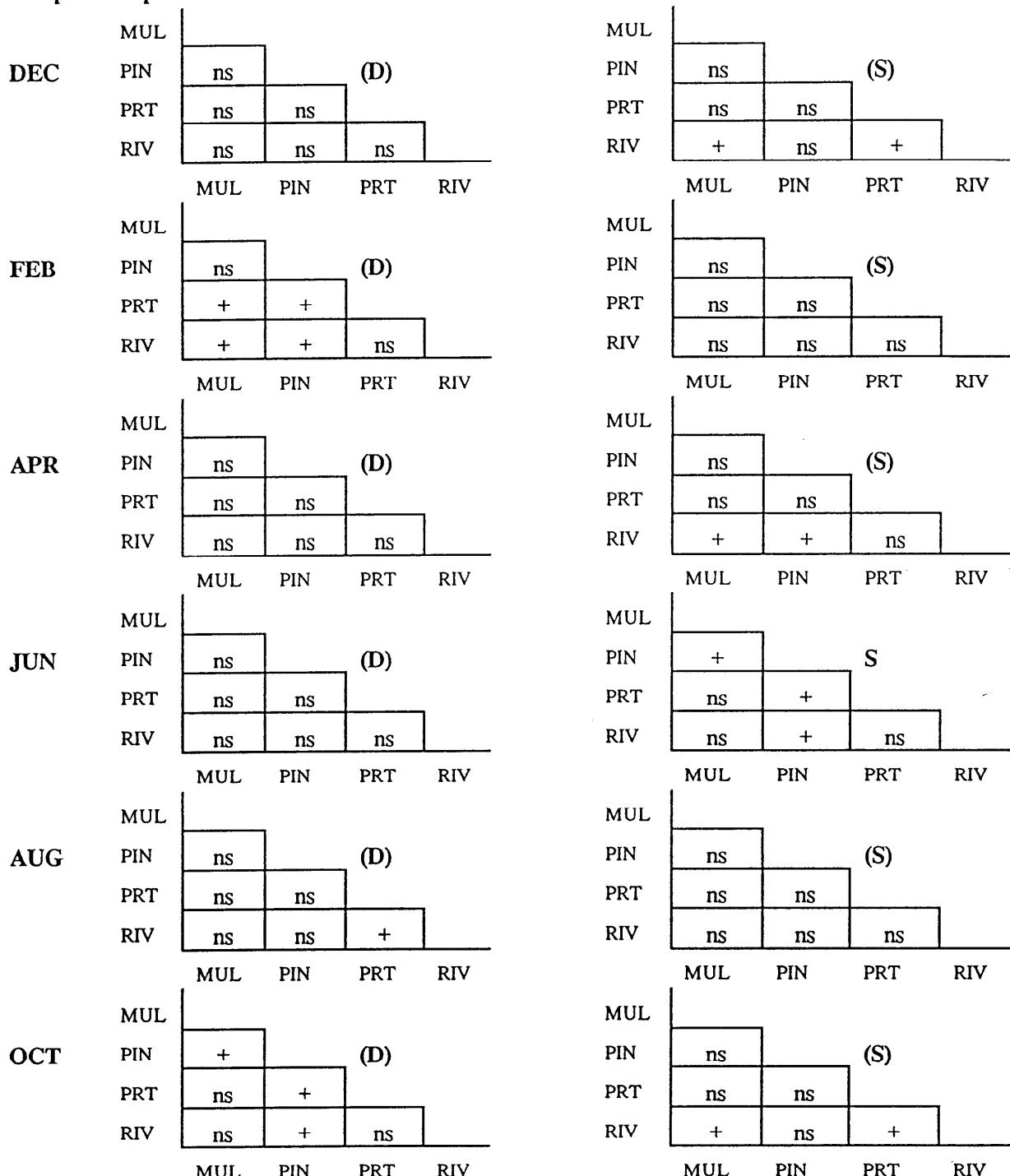
Multiple Comparison



		DEC	FEB	APR	JUN	AUG	OCT
t-test	S/D	(ns)	ns	ns	(ns)	(ns)	+++
MUL	S/D	(+)	+++	(ns)	ns	ns	ns
PIN	S/D	(ns)	(ns)	ns	(++)	(ns)	ns
PRT	S/D	(ns)	(ns)	ns	(++)	(ns)	ns
RIV	S/D	(ns)	ns	+	+	+	ns

Appendix Table B.9. Multiple comparison analyses and t-tests for RATIO OF TOTAL EPIPHYTE BIOMASS TO ABOVE-GROUND *THALASSIA* BIOMASS.

Multiple Comparison

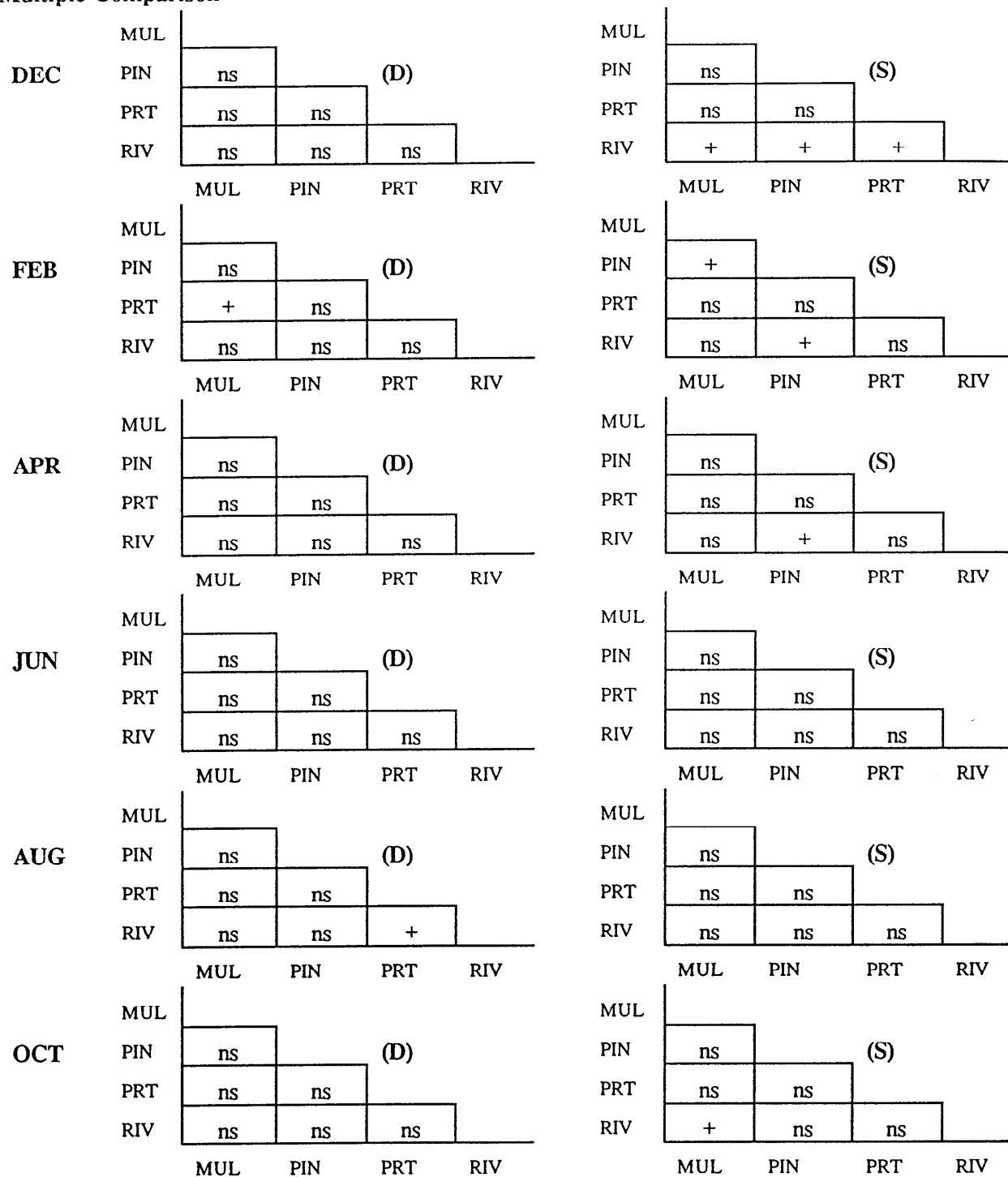


t-test

		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	(+++)	ns	(+++)	+++	(+++)	++
PIN	S/D	(+++)	ns	ns	+++	+++	(+++)
PRT	S/D	ns	(+++)	(+++)	ns	+++	+
RIV	S/D	(+++)	+++	ns	+++	(+++)	(+++)

Appendix Table B. 10. Multiple comparison analyses and t-tests for RATIO OF ASH FREE EPIPHYTE BIOMASS TO ABOVE-GROUND **THALASSIA** BIOMASS.

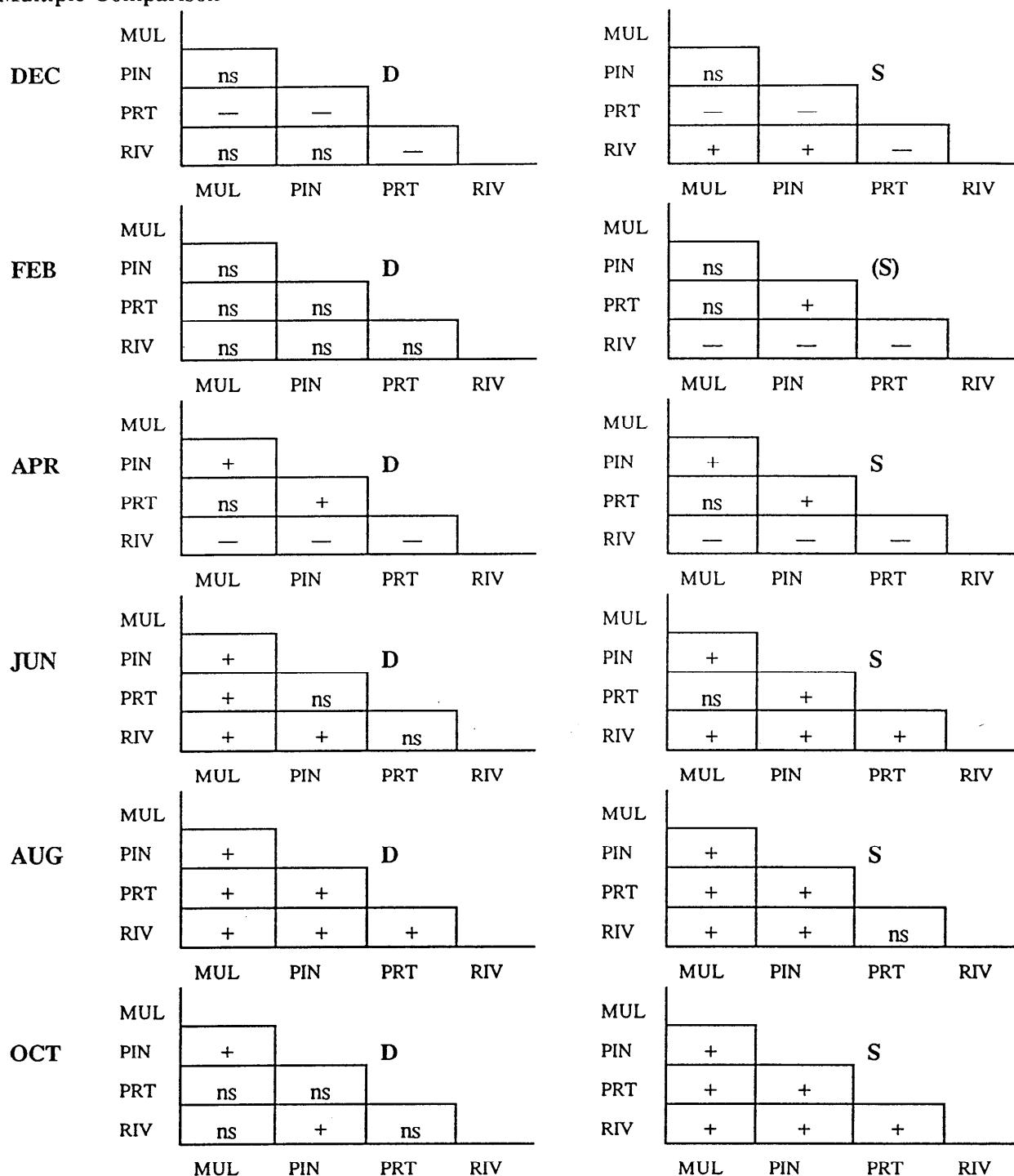
Multiple Comparison



t-test		DEC	FEB	APR	JUN	AUG	OCT
	S/D	(+++)	ns	(+++)	(+++)	(+++)	(+++)
PIN	S/D	+	(+++)	(+++)	(+++)	(+++)	(+++)
PRT	S/D	(ns)	(+++)	(+++)	ns	(+++)	(+++)
RIV	S/D	(+++)	++	ns	++	(+++)	(+++)

Appendix Table B. 11. Multiple comparison analyses and t-tests for TOTAL DAILY PAR (ADJUSTED FOR EPIPHYTE ATTENUATION).

Multiple Comparison



t-test		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	++	+++	+++	+++	+++	+++
PIN	S/D	+++	+++	+++	+++	+++	+++
PRT	S/D	—	+++	+++	+++	+++	+++
RIV	S/D	+++	—	—	+++	+++	+++

Appendix Table B. 12. Multiple comparison analyses and t-tests for AVERAGE DAILY LIGHT PERIOD ABOVE I.,

Multiple Comparison

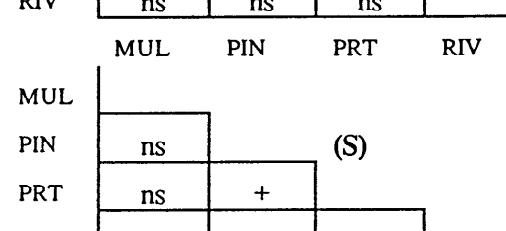
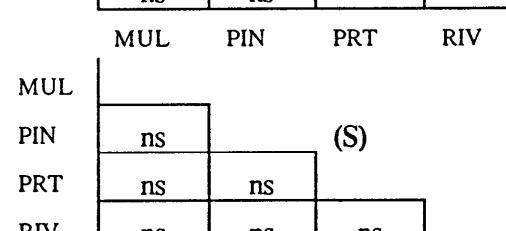
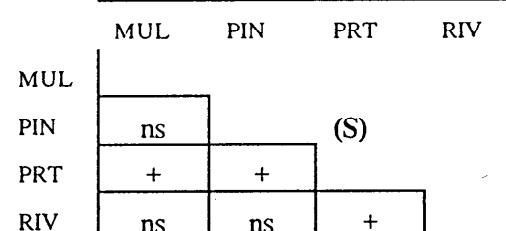
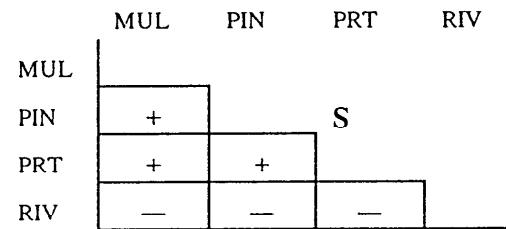
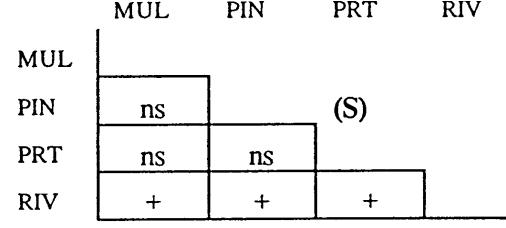
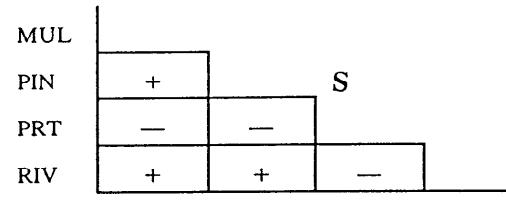
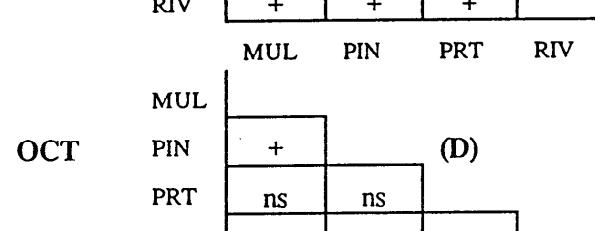
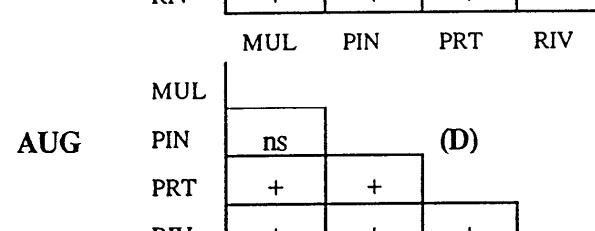
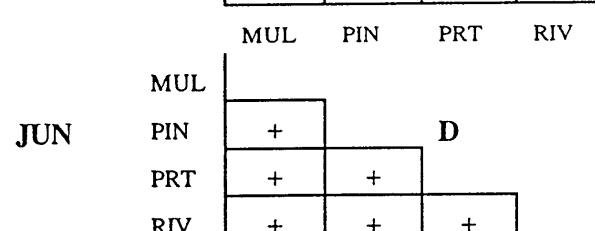
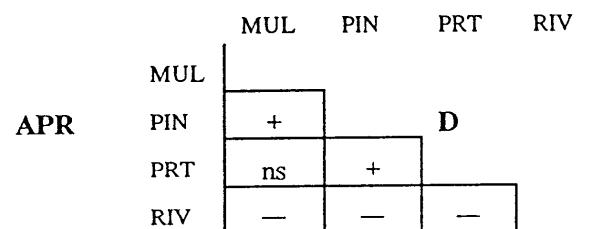
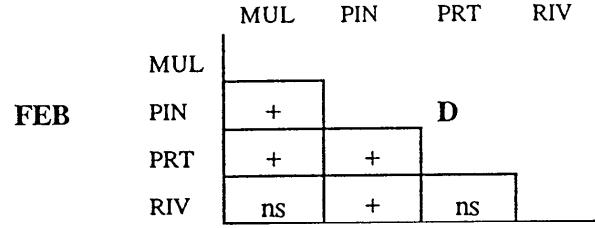
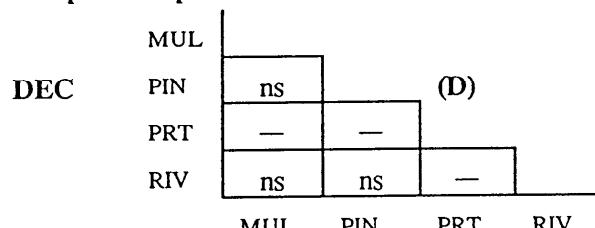
		MUL	PIN	PRT	RIV
		PIN	ns	D	
		PRT	—	—	
		RIV	ns	ns	—
DEC		MUL	PIN	PRT	RIV
		PIN	ns	D	
		PRT	—	—	
		RIV	ns	ns	—
FEB		MUL	PIN	PRT	RIV
		PIN	ns	D	
		PRT	ns	ns	
		RIV	ns	ns	ns
APR		MUL	PIN	PRT	RIV
		PIN	+	(D)	
		PRT	ns	+	
		RIV	—	—	—
JUN		MUL	PIN	PRT	RIV
		PIN	ns	(D)	
		PRT	+	+	
		RIV	ns	ns	+
AUG		MUL	PIN	PRT	RIV
		PIN	+	(D)	
		PRT	+	+	
		RIV	+	+	+
OCT		MUL	PIN	PRT	RIV
		PIN	+	(D)	
		PRT	ns	ns	
		RIV	ns	+	+

		MUL	PIN	PRT	RIV
		PIN	+	S	
		PRT	—	—	
		RIV	+	+	—
MUL	PIN	MUL	PIN	PRT	RIV
		PIN	ns	(S)	
		PRT	ns	ns	
		RIV	+	ns	+
MUL	PIN	MUL	PIN	PRT	RIV
		PIN	+	(S)	
		PRT	ns	+	
		RIV	—	—	—
MUL	PIN	MUL	PIN	PRT	RIV
		PIN	ns	(S)	
		PRT	ns	ns	
		RIV	ns	ns	ns
MUL	PIN	MUL	PIN	PRT	RIV
		PIN	ns	(S)	
		PRT	ns	ns	
		RIV	ns	ns	ns
MUL	PIN	MUL	PIN	PRT	RIV
		PIN	ns	(S)	
		PRT	ns	+	
		RIV	+	+	ns

t-test		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	+++	+++	++	+++	+++	+++
PIN	S/D	+++	+++	+++	+++	+++	+++
PRT	S/D	—	+++	+++	+++	+++	+++
RIV	S/D	+++	(+++)	—	+++	+++	+++

Appendix Table B. 13. Multiple comparison analyses and t-tests for AVERAGE DAILY LIGHT PERIOD ABOVE I.,

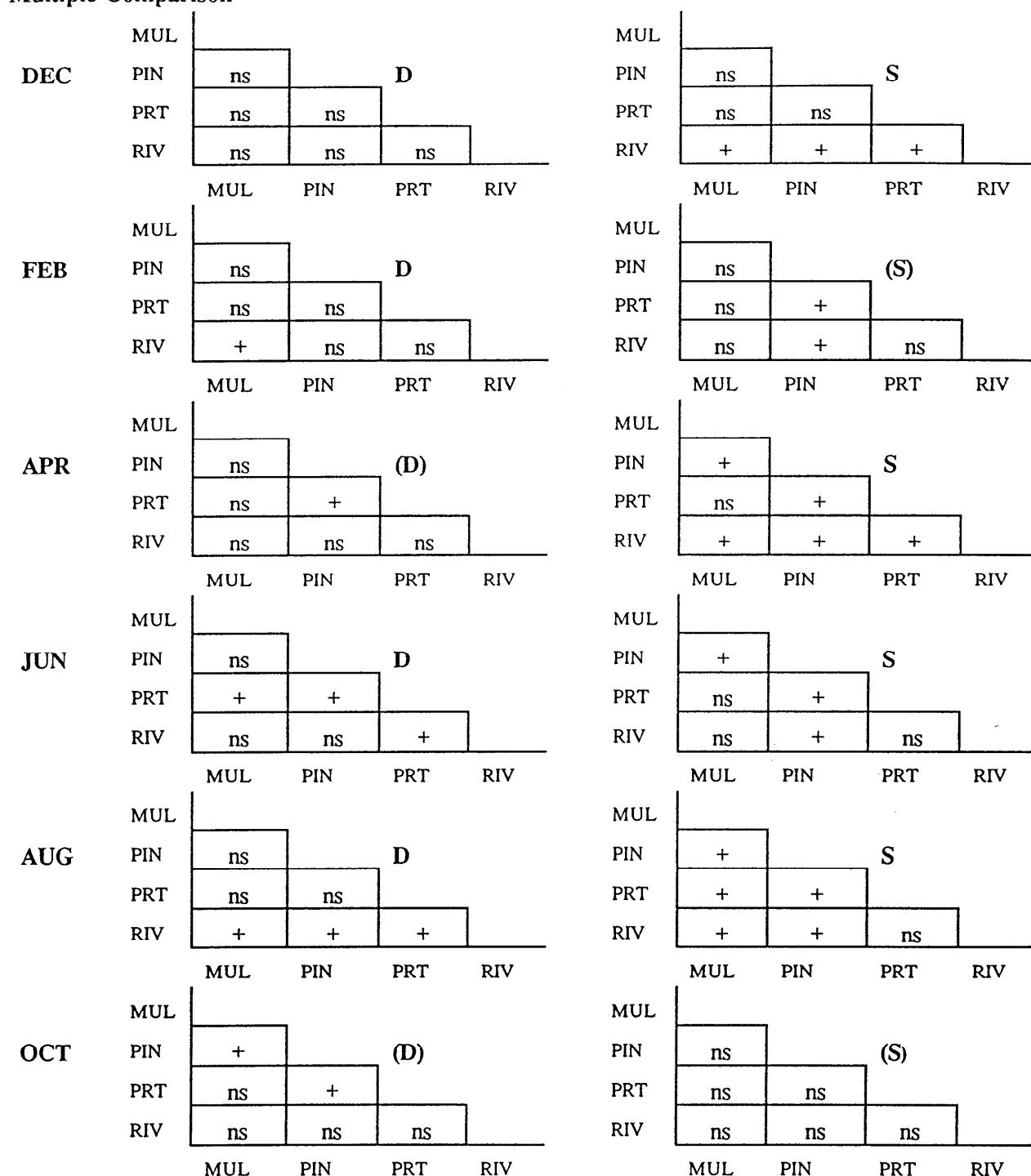
Multiple Comparison



t-test		DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	+++	+++	+++	ns	+++	+++
PIN	S/D	+++	+++	+++	+++	+++	+++
PRT	S/D	—	+++	+++	+++	+++	+++
RIV	S/D	+++	+++	—	++	+++	+

Appendix Table B. 14. Multiple comparison analyses and t-tests for PERCENT EPIPHYTE ATTENUATION.

Multiple Comparison

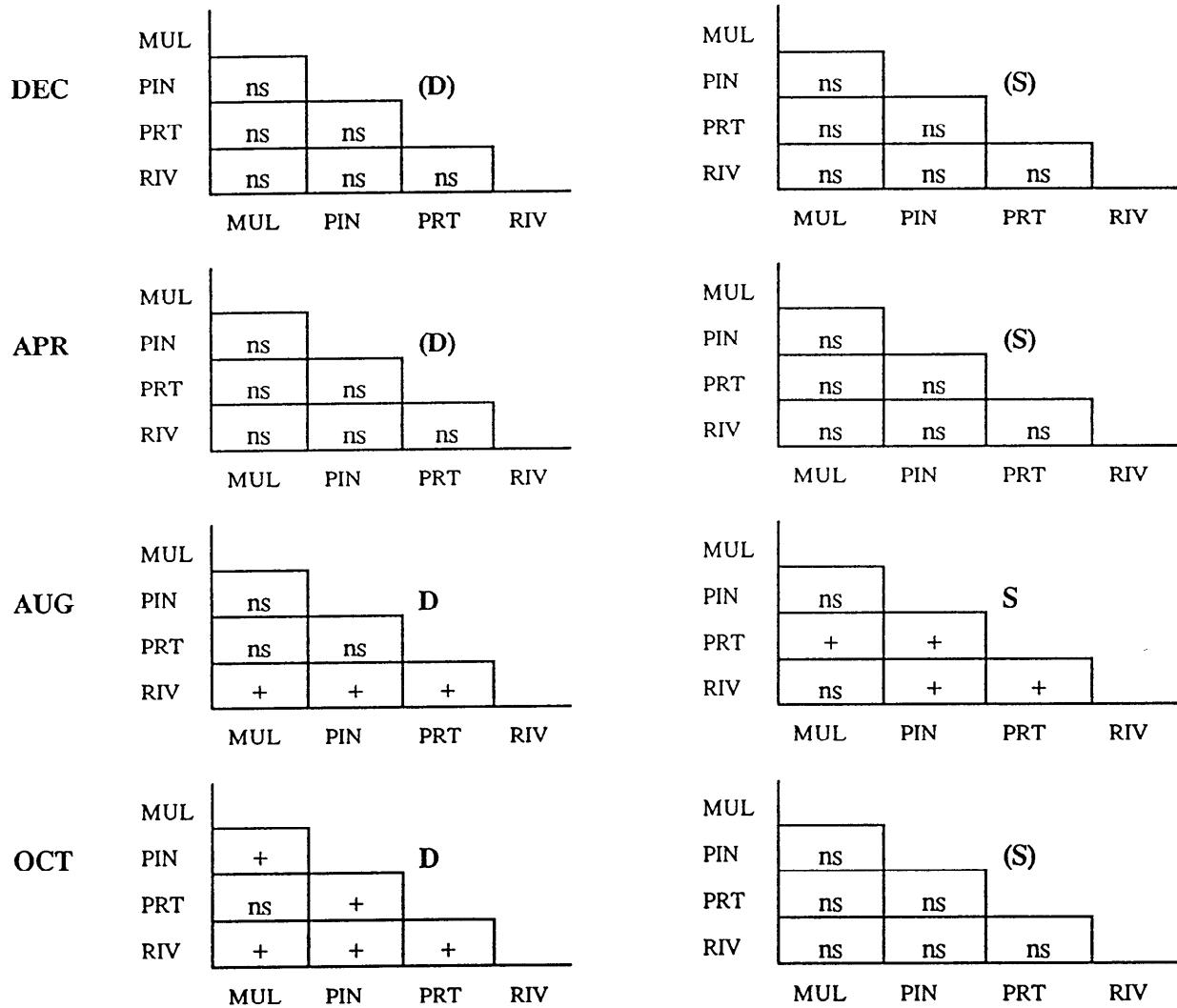


t-test

	DEC	FEB	APR	JUN	AUG	OCT
MUL	S/D	ns	ns	+++	(+++)	++
PIN	S/D	ns	ns	(+++)	+++	(+++)
PRT	S/D	ns	++	(+++)	+++	ns
RIV	S/D	++	+++	ns	(+++)	(+++)

Appendix Table B. 15. Multiple comparison analyses and t-tests for CORES-ABOVE-GROUND BIOMASS.

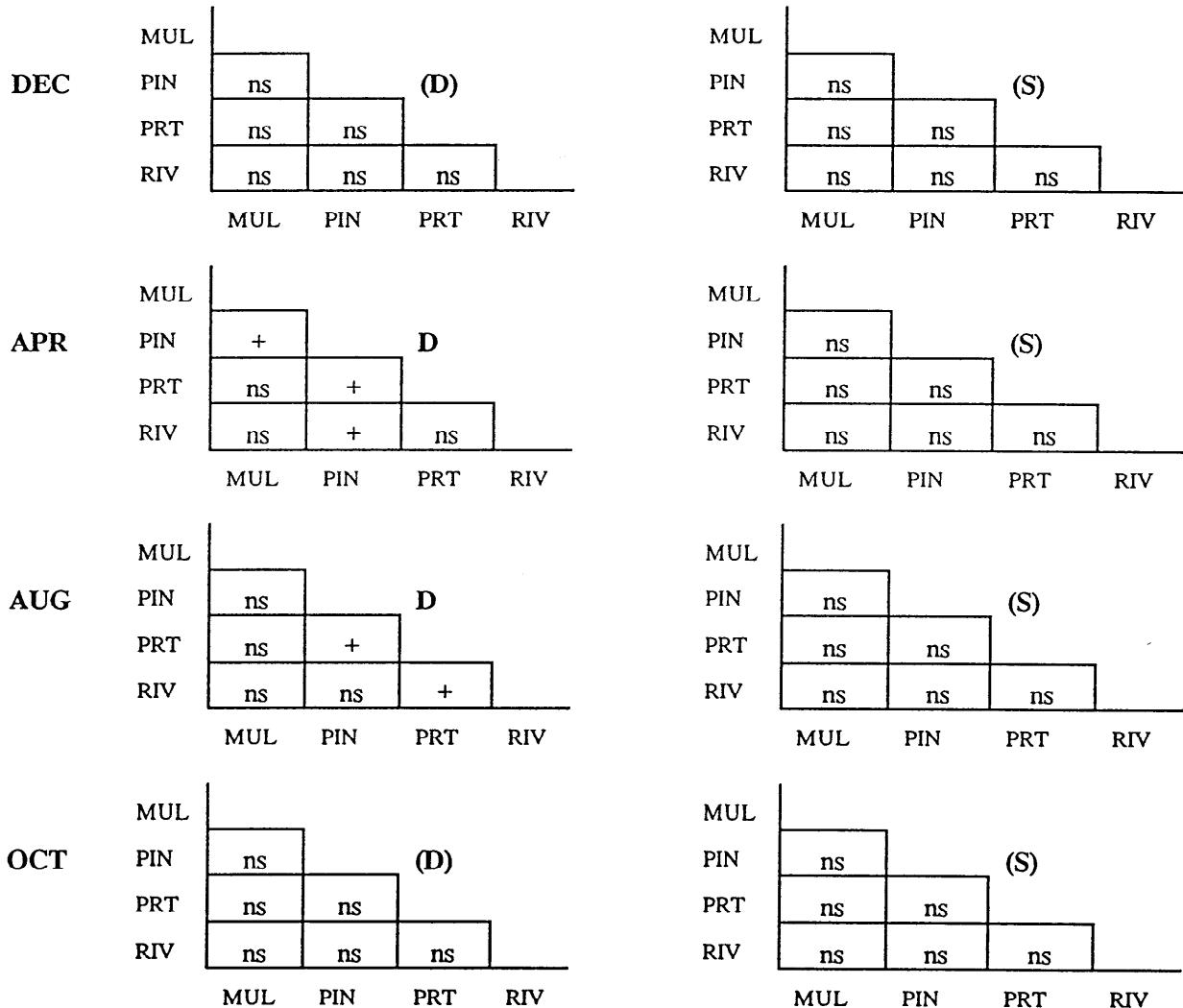
Multiple Comparison



		DEC	APR	AUG	OCT
t-test	S/D	(+++)	+++	(+++)	(+++)
MUL	S/D	(+++)	(+++)	ns	+++
PIN	S/D	(+++)	(+++)	ns	+++
PRT	S/D	+	+++	(+++)	(+++)
RIV	S/D	+++	(+++)	(+++)	(+++)

Appendix Table B. 16. Multiple comparison analyses and t-tests for CORES-BELOW-GROUND BIOMASS.

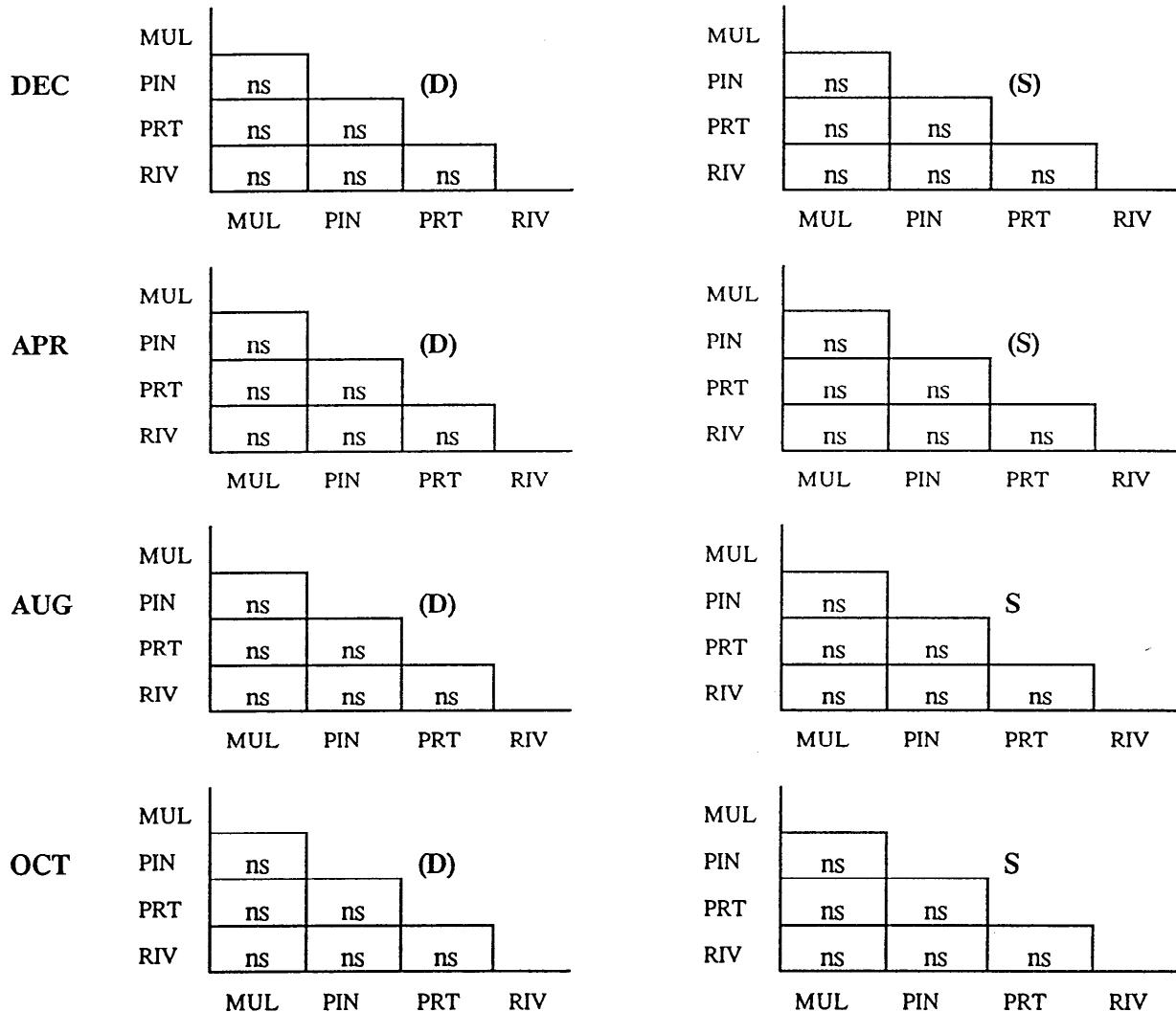
Multiple Comparison



t-test		DEC	APR	AUG	OCT
MUL	S/D	(+++)	(+++)	(+++)	(+++)
PIN	S/D	(+++)	(+++)	(+++)	(+++)
PRT	S/D	(+++)	(+++)	+++	+++
RIV	S/D	(+++)	(+++)	(+++)	(+++)

Appendix Table B.17. Multiple comparison analyses and t-tests for ABOVE- TO BELOW-GROUND BIOMASS RATIO.

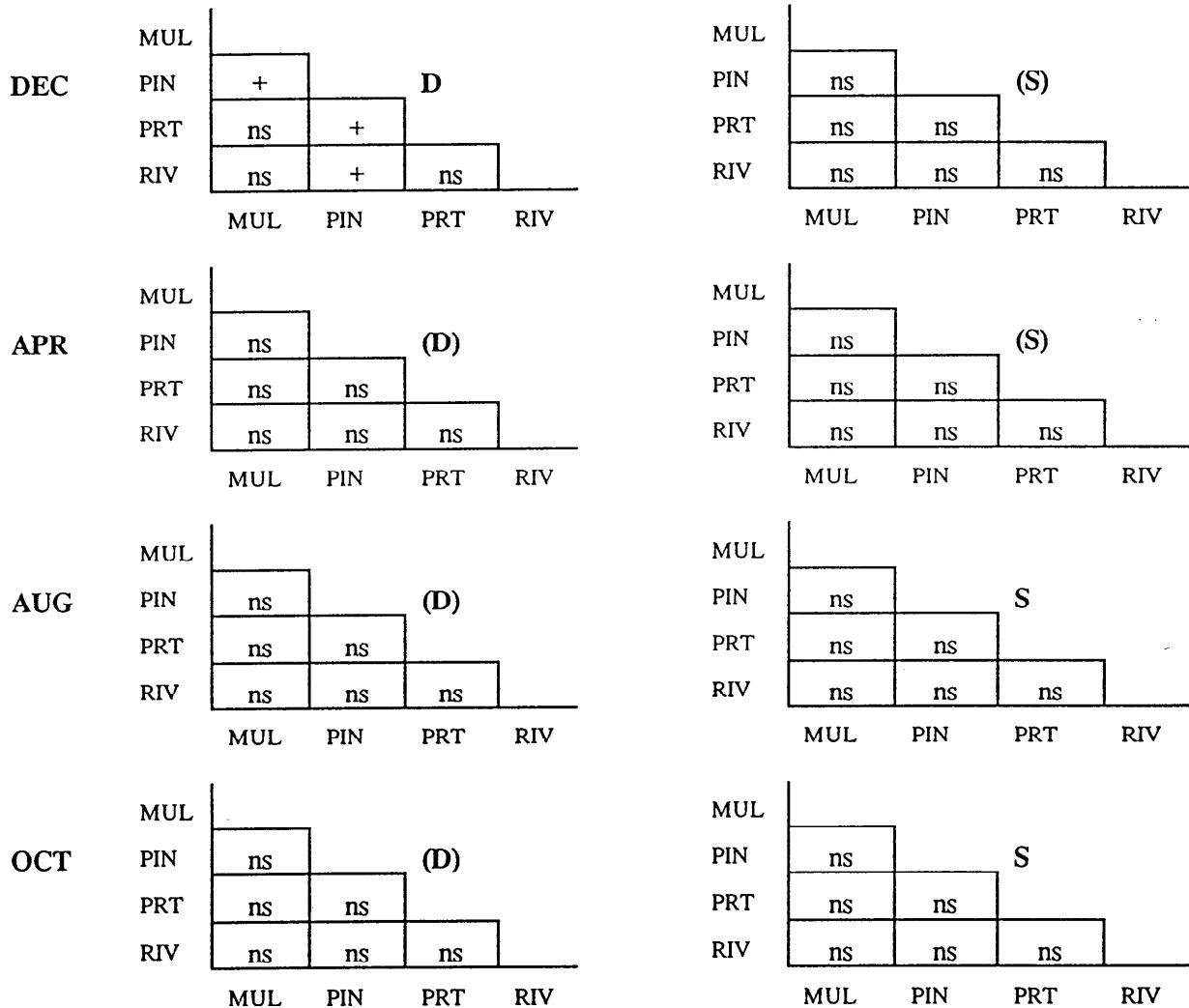
Multiple Comparison



t-test		DEC	APR	AUG	OCT
MUL	S/D	+	ns	(ns)	ns
PIN	S/D	(+++)	(+)	(+++)	(+++)
PRT	S/D	(ns)	(ns)	+	(+++)
RIV	S/D	(+++)	(+++)	ns	(++)

Appendix Table B. 18. Multiple comparison analyses and t-tests for BLADE PERCENT OF TOTAL BIOMASS.

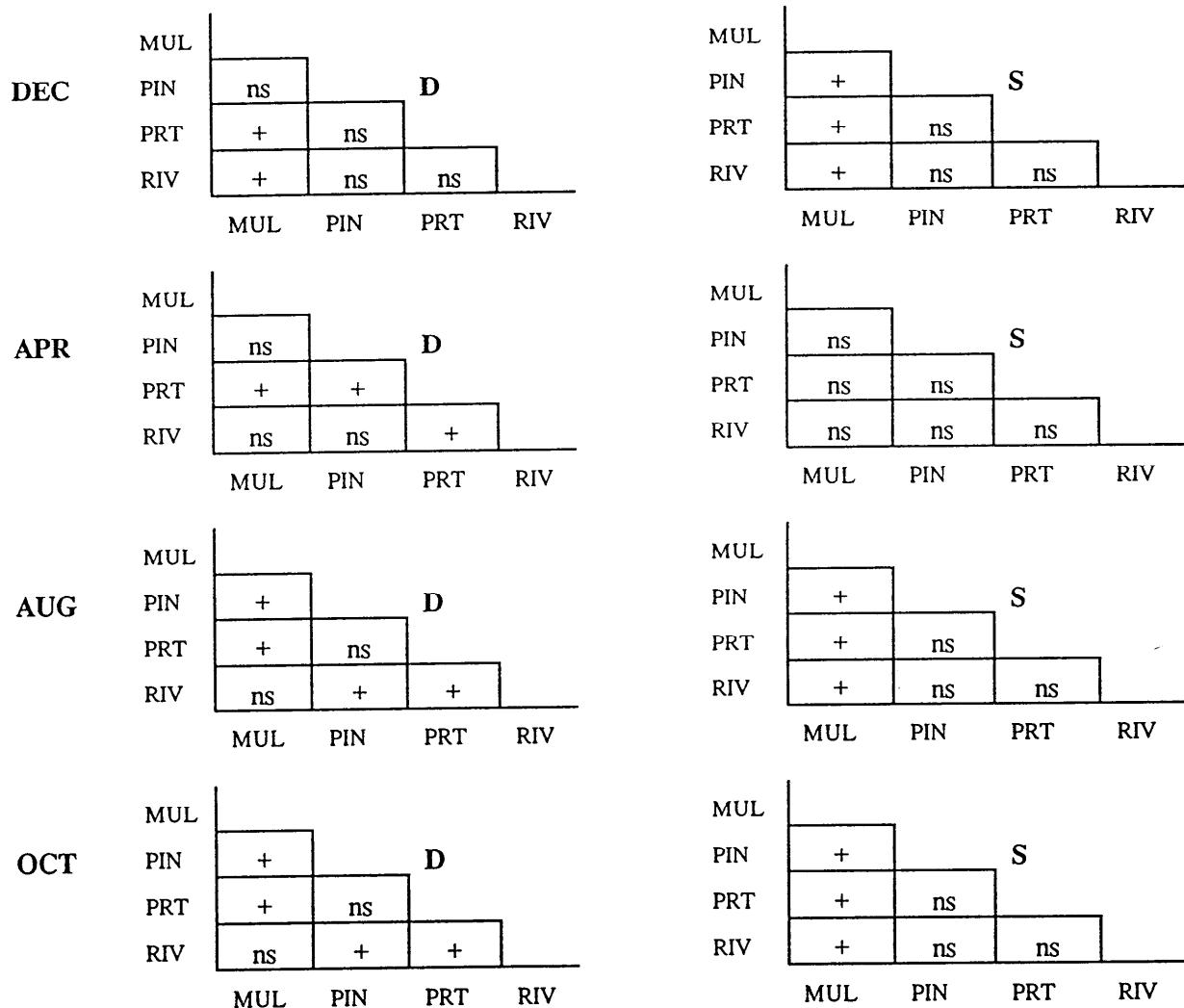
Multiple Comparison



		DEC	APR	AUG	OCT
t-test	S/D	+	ns	(ns)	ns
MUL	S/D	++	ns	+++	++
PIN	S/D	ns	(ns)	++	+++
PRT	S/D	(+++)	ns	ns	(++)
RIV	S/D				

Appendix Table B. 19. Multiple comparison analyses and t-tests for SHOOT PERCENT OF TOTAL BIOMASS.

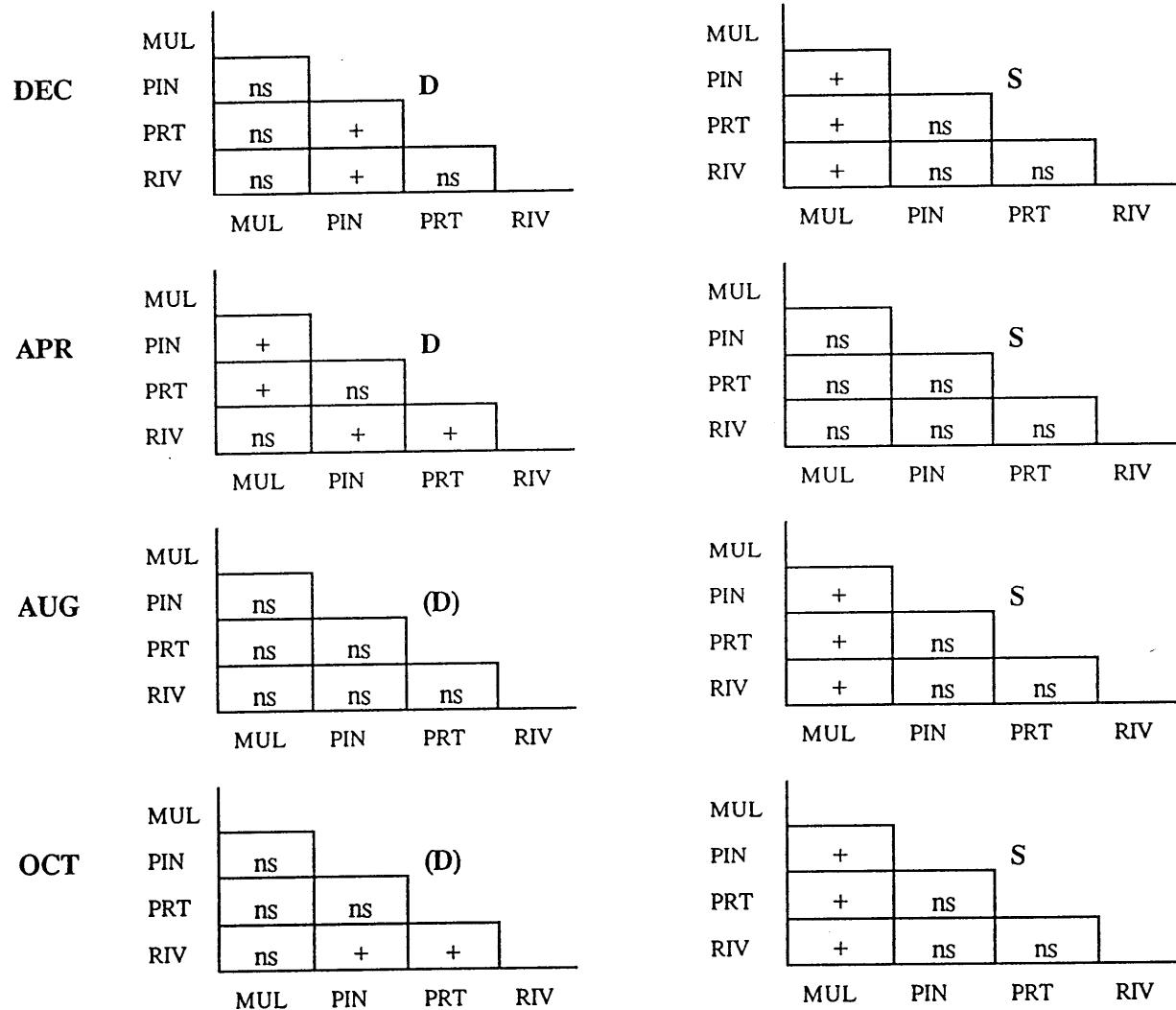
Multiple Comparison



t-test		DEC	APR	AUG	OCT
MUL	S/D	++	ns	(+)	ns
PIN	S/D	+	ns	+	ns
PRT	S/D	++	ns	(ns)	(ns)
RIV	S/D	+++	+++	+++	(++)

Appendix Table B.20. Multiple comparison analyses and t-tests for ROOT PERCENT OF TOTAL BIOMASS.

Multiple Comparison



t-test		DEC	APR	AUG	OCT
MUL	S/D	++	ns	ns	ns
PIN	S/D	ns	ns	+++	ns
PRT	S/D	ns	ns	ns	ns
RIV	S/D	ns	++	+++	(++)

Appendix C

Raw Data

Appendix Table C.1. Mean and standard deviations for 16 blade parameter analyses for each station, depth and date.

	MUL S	PIN S	PRT S	RIV S	MUL D	PIN D	PRT D	RIV D
ASH FREE EPIPHYTE:ABOVE-GROUND BIOMASS RATIO								
Jan	0.180 ± 0.079	0.160 ± 0.052	0.229 ± 0.114	0.030 ± 0.048	0.140 ± 0.070	0.270 ± 0.157	0.510 ± 0.664	0.220 ± 0.130
Mar	0.109 ± 0.070	0.200 ± 0.105	0.110 ± 0.032	0.090 ± 0.032	0.090 ± 0.099	0.130 ± 0.048	0.200 ± 0.050	0.180 ± 0.079
May	0.130 ± 0.048	0.210 ± 0.074	0.122 ± 0.044	0.050 ± 0.053	0.130 ± 0.067	0.170 ± 0.106	0.110 ± 0.032	0.080 ± 0.042
Jun	0.110 ± 0.032	0.140 ± 0.052	0.100 ± 0.000	0.110 ± 0.032	0.050 ± 0.053	0.020 ± 0.042	0.100 ± 0.000	0.040 ± 0.052
Aug	0.100 ± 0.000	0.110 ± 0.032	0.080 ± 0.042	0.070 ± 0.048	0.033 ± 0.050	0.020 ± 0.042	0.000 ± 0.000	0.120 ± 0.123
Oct	0.100 ± 0.000	0.056 ± 0.053	0.060 ± 0.052	0.010 ± 0.032	0.020 ± 0.042	0.000 ± 0.000	0.040 ± 0.052	0.030 ± 0.048
ABOVE-GROUND BIOMASS (g/dry wt/m²)								
Jan	33.66 ± 12.60	16.98 ± 4.71	22.83 ± 8.70	50.05 ± 9.76	3.96 ± 1.28	5.59 ± 2.10	3.61 ± 1.08	5.86 ± 1.69
Mar	48.70 ± 18.31	24.89 ± 5.68	22.44 ± 10.61	67.23 ± 14.27	4.27 ± 1.49	7.50 ± 2.84	7.87 ± 3.17	8.04 ± 2.06
May	87.25 ± 30.74	79.39 ± 26.37	88.74 ± 21.30	213.55 ± 66.40	16.74 ± 4.94	32.50 ± 13.13	22.74 ± 8.74	17.00 ± 4.58
Jun	29.21 ± 9.81	34.84 ± 10.95	105.01 ± 44.46	125.46 ± 34.59	19.82 ± 5.36	21.65 ± 9.97	15.19 ± 2.70	17.01 ± 6.08
Aug	48.53 ± 19.11	32.98 ± 11.40	73.32 ± 37.90	65.23 ± 25.86	12.10 ± 3.11	27.22 ± 11.45	17.11 ± 9.61	6.53 ± 2.43
Oct	33.34 ± 14.17	29.24 ± 7.08	23.75 ± 9.66	25.05 ± 16.66	4.97 ± 1.82	10.70 ± 4.42	12.28 ± 17.47	3.32 ± 1.76
ASH FREE EPIPHYTE BIOMASS AS PERCENT OF TOTAL EPIPHYTE BIOMASS								
Jan	44.31 ± 11.63	40.93 ± 10.51	26.96 ± 9.52	44.69 ± 17.70	20.83 ± 8.09	20.73 ± 7.29	26.35 ± 16.70	21.56 ± 12.78
Mar	44.84 ± 11.76	54.99 ± 6.70	41.13 ± 22.89	16.50 ± 8.93	34.07 ± 15.22	32.14 ± 11.22	11.32 ± 4.26	7.81 ± 2.97
May	27.76 ± 4.56	34.82 ± 2.27	43.11 ± 7.52	29.20 ± 14.31	13.28 ± 5.20	29.74 ± 8.81	37.79 ± 11.47	34.08 ± 8.65
Jun	21.89 ± 4.36	20.35 ± 2.46	24.28 ± 4.13	25.54 ± 2.12	26.19 ± 10.01	35.32 ± 6.78	28.68 ± 7.01	41.31 ± 11.11
Aug	31.53 ± 10.60	21.12 ± 4.17	22.05 ± 3.86	28.88 ± 4.74	26.80 ± 13.42	36.09 ± 12.33	26.36 ± 9.61	31.08 ± 11.02
Oct	29.98 ± 10.13	30.32 ± 16.49	29.19 ± 9.55	33.98 ± 12.44	32.19 ± 9.22	42.53 ± 10.78	35.61 ± 15.86	35.75 ± 29.84
AVERAGE DAILY PAR (E/m²/day)								
Jan	9.28 ± 1.93	10.81 ± 1.92	N/A ± N/A	16.81 ± 3.06	6.60 ± 1.85	4.69 ± 2.80	N/A ± N/A	6.58 ± 2.74
Mar	18.20 ± 2.58	12.54 ± 2.68	18.81 ± 3.23	1.80 ± 0.16	9.83 ± 3.01	8.56 ± 0.85	9.03 ± 2.38	9.41 ± 3.03
May	23.75 ± 5.31	9.58 ± 1.56	22.10 ± 2.41	N/A ± N/A	12.55 ± 3.78	5.72 ± 1.33	11.05 ± 2.00	N/A ± N/A
Jun	23.10 ± 4.71	12.92 ± 1.60	20.59 ± 1.53	29.12 ± 4.28	11.57 ± 1.15	8.45 ± 0.69	8.86 ± 0.77	9.49 ± 0.64
Aug	13.43 ± 1.91	5.55 ± 0.96	10.48 ± 1.23	11.45 ± 1.13	6.07 ± 0.62	4.47 ± 0.39	7.01 ± 0.49	2.79 ± 0.86
Oct	12.36 ± 1.85	7.14 ± 0.67	15.03 ± 1.43	17.72 ± 4.95	5.81 ± 0.53	3.98 ± 0.07	4.77 ± 0.72	5.85 ± 2.11
CARBOHYDRATES (mg/g)								
Jan	283.7 ± 144.5	216.0 ± 78.2	264.5 ± 66.5	264.0 ± 99.9	368.4 ± 73.5	291.7 ± 95.8	342.7 ± 76.3	347.5 ± 102.5
Mar	280.6 ± 88.4	256.1 ± 57.0	182.6 ± 60.2	293.2 ± 108.4	336.9 ± 104.1	305.7 ± 95.7	373.2 ± 64.5	356.2 ± 66.8
May	267.2 ± 97.4	212.7 ± 68.0	255.3 ± 80.7	294.4 ± 110.1	330.2 ± 103.9	302.1 ± 106.5	379.9 ± 83.6	326.9 ± 112.0
Jun	200.1 ± 98.7	134.3 ± 26.5	274.2 ± 107.9	217.5 ± 30.3	247.3 ± 107.2	317.0 ± 93.7	310.8 ± 79.0	345.1 ± 62.9
Aug	288.6 ± 117.3	211.2 ± 64.3	281.7 ± 52.4	293.8 ± 91.8	383.1 ± 103.0	404.1 ± 42.5	312.0 ± 138.6	341.4 ± 107.9
Oct	221.9 ± 115.1	243.3 ± 81.2	320.6 ± 63.5	243.5 ± 112.6	411.2 ± 46.0	391.3 ± 75.9	336.4 ± 91.2	311.4 ± 83.8
EPIPHYTIC ATTENUATION (%)								
Jan	57.03 ± 8.91	50.75 ± 8.75	61.98 ± 12.05	24.45 ± 13.76	47.84 ± 14.62	64.60 ± 21.14	67.31 ± 19.08	52.42 ± 19.80
Mar	34.06 ± 9.36	46.74 ± 11.38	26.62 ± 12.59	23.88 ± 6.91	32.37 ± 20.71	40.17 ± 5.91	47.68 ± 13.79	54.25 ± 14.74
May	46.33 ± 11.99	56.42 ± 7.08	44.11 ± 6.09	21.06 ± 7.43	50.59 ± 14.90	42.20 ± 13.41	39.27 ± 11.01	24.13 ± 4.10

Appendix Table C.1. Continued.

	MUL S	PIN S	PRT S	RIV S	MUL D	PIN D	PRT D	RIV D
Jun	41.82 ± 11.87	50.87 ± 6.08	35.46 ± 4.79	36.93 ± 9.27	22.91 ± 7.63	20.11 ± 6.51	30.07 ± 6.09	22.79 ± 5.18
Aug	38.72 ± 8.72	49.19 ± 8.79	30.77 ± 8.13	27.63 ± 7.11	21.78 ± 7.96	18.07 ± 7.21	10.81 ± 6.27	33.56 ± 20.50
Oct	31.96 ± 10.18	26.35 ± 6.87	21.42 ± 7.48	25.13 ± 20.93	20.21 ± 7.29	6.74 ± 1.65	22.17 ± 11.71	17.77 ± 29.62
EPIPHYTE TO ABOVE-GROUND BIOMASS RATIO								
Jan	0.462 ± 0.184	0.420 ± 0.143	0.963 ± 0.551	0.149 ± 0.112	0.789 ± 0.422	1.449 ± 0.961	2.219 ± 2.259	1.566 ± 1.522
Mar	0.312 ± 0.188	0.380 ± 0.176	0.349 ± 0.237	0.612 ± 0.387	0.324 ± 0.216	0.384 ± 0.147	1.987 ± 0.981	3.016 ± 1.903
May	0.431 ± 0.128	0.569 ± 0.173	0.350 ± 0.171	0.178 ± 0.094	0.999 ± 0.912	0.676 ± 0.432	0.314 ± 0.225	0.178 ± 0.067
Jun	0.470 ± 0.122	0.695 ± 0.185	0.394 ± 0.125	0.406 ± 0.134	0.246 ± 0.111	0.124 ± 0.057	0.300 ± 0.140	0.159 ± 0.116
Aug	0.275 ± 0.196	0.557 ± 0.193	0.300 ± 0.099	0.206 ± 0.063	0.248 ± 0.234	0.113 ± 0.081	0.095 ± 0.101	0.408 ± 0.480
Oct	0.296 ± 0.132	0.287 ± 0.302	0.199 ± 0.086	0.099 ± 0.040	0.124 ± 0.068	0.032 ± 0.015	0.115 ± 0.079	0.146 ± 0.182
AVERAGE HOURS PER DAY >IC								
Jan	8.16 ± 0.21	8.82 ± 0.24	N/A ± N/A	9.45 ± 0.23	7.56 ± 0.40	6.91 ± 1.43	N/A ± N/A	8.10 ± 0.70
Mar	10.46 ± 0.12	10.13 ± 0.35	10.24 ± 0.29	0.78 ± 0.00	8.90 ± 0.57	9.50 ± 0.14	8.95 ± 0.36	8.98 ± 0.64
May	11.59 ± 0.29	10.20 ± 0.41	11.90 ± 0.13	N/A ± N/A	10.10 ± 0.72	7.72 ± 1.03	10.37 ± 0.45	N/A ± N/A
Jun	13.20 ± 0.22	13.42 ± 0.07	13.90 ± 0.03	12.90 ± 0.04	13.24 ± 0.08	12.39 ± 0.10	12.47 ± 0.09	12.99 ± 0.08
Aug	10.40 ± 0.30	7.61 ± 0.60	10.28 ± 0.30	10.57 ± 0.08	7.26 ± 0.32	6.64 ± 0.24	9.24 ± 0.12	5.20 ± 1.26
Oct	9.52 ± 0.20	8.87 ± 0.08	9.79 ± 0.05	9.70 ± 0.68	8.27 ± 0.19	7.66 ± 0.02	7.89 ± 0.29	7.58 ± 2.67
AVERAGE HOURS PER DAY >IK								
Jan	5.44 ± 0.65	6.17 ± 0.55	N/A ± N/A	7.49 ± 0.41	4.03 ± 0.81	2.62 ± 2.20	N/A ± N/A	4.44 ± 1.56
Mar	8.06 ± 0.40	7.24 ± 1.02	8.04 ± 0.52	0.72 ± 0.01	5.56 ± 1.27	5.51 ± 0.38	5.76 ± 0.94	5.43 ± 1.13
May	9.83 ± 0.51	6.48 ± 1.40	9.10 ± 0.37	N/A ± N/A	7.99 ± 1.66	2.12 ± 0.65	5.41 ± 1.59	N/A ± N/A
Jun	11.72 ± 0.43	8.09 ± 0.35	11.73 ± 0.14	10.59 ± 0.23	6.64 ± 0.35	6.18 ± 0.40	8.76 ± 0.31	7.13 ± 0.45
Aug	6.22 ± 0.42	3.38 ± 0.64	6.24 ± 0.55	6.43 ± 0.35	3.65 ± 0.35	2.40 ± 0.20	4.51 ± 0.25	1.38 ± 0.71
Oct	7.03 ± 0.40	5.35 ± 0.38	7.52 ± 0.20	7.44 ± 1.71	4.09 ± 0.49	2.03 ± 0.09	3.06 ± 0.94	4.28 ± 1.54
LEAF AREA PER SHOOT (cm²)								
Jan	19.46 ± 7.20	18.66 ± 5.35	16.51 ± 6.06	27.33 ± 5.65	11.62 ± 3.33	14.27 ± 5.52	18.47 ± 5.28	15.32 ± 4.31
Mar	26.61 ± 10.14	23.06 ± 5.45	21.05 ± 9.66	32.77 ± 6.49	13.39 ± 4.90	20.15 ± 7.82	22.06 ± 8.33	20.71 ± 6.19
May	56.93 ± 21.76	59.28 ± 18.84	78.85 ± 20.49	79.67 ± 27.14	35.77 ± 15.18	69.63 ± 28.30	81.88 ± 25.26	55.82 ± 15.12
Jun	49.15 ± 16.03	53.31 ± 17.57	80.16 ± 31.89	82.97 ± 20.29	54.01 ± 12.85	62.78 ± 28.91	56.46 ± 10.32	40.97 ± 15.56
Aug	27.54 ± 10.38	48.01 ± 18.81	44.51 ± 23.31	49.03 ± 17.04	26.78 ± 5.57	78.17 ± 32.92	27.41 ± 14.76	22.87 ± 9.54
Oct	27.97 ± 11.99	39.15 ± 10.14	29.69 ± 11.02	33.55 ± 23.04	21.19 ± 7.85	56.71 ± 22.61	21.67 ± 7.82	11.80 ± 6.26
LEAF AREA INDEX (m²/m²)								
Jan	0.683 ± 0.253	0.322 ± 0.092	0.463 ± 0.170	0.838 ± 0.173	0.071 ± 0.020	0.092 ± 0.036	0.066 ± 0.019	0.108 ± 0.030
Mar	0.940 ± 0.358	0.489 ± 0.115	0.484 ± 0.222	1.086 ± 0.215	0.073 ± 0.027	0.131 ± 0.051	0.145 ± 0.055	0.136 ± 0.041
May	1.776 ± 0.679	1.598 ± 0.508	2.258 ± 0.587	3.323 ± 1.132	0.236 ± 0.100	0.571 ± 0.232	0.458 ± 0.142	0.385 ± 0.104
Jun	0.556 ± 0.181	0.830 ± 0.273	2.267 ± 0.901	2.755 ± 0.674	0.422 ± 0.100	0.490 ± 0.225	0.314 ± 0.057	0.392 ± 0.149
Aug	0.962 ± 0.363	0.837 ± 0.328	1.410 ± 0.738	1.384 ± 0.481	0.206 ± 0.043	0.664 ± 0.280	0.300 ± 0.161	0.130 ± 0.054
Oct	0.754 ± 0.323	0.658 ± 0.170	0.470 ± 0.175	0.452 ± 0.311	0.094 ± 0.035	0.259 ± 0.103	0.142 ± 0.051	0.064 ± 0.034

	MUL S	PIN S	PRT S	RIV S	MUL D	PIN D	PRT D	RIV D
LEAF RELATIVE GROWTH RATE (mg dry wt/g dry wt/day)								
Jan	2.40 ± 2.24	2.56 ± 2.18	3.54 ± 3.94	2.74 ± 2.91	1.90 ± 2.40	0.84 ± 1.43	3.68 ± 2.88	1.81 ± 1.68
Mar	13.94 ± 4.26	21.27 ± 9.52	13.56 ± 9.48	18.63 ± 4.26	13.35 ± 9.17	8.08 ± 8.16	20.27 ± 5.90	17.58 ± 5.34
May	31.22 ± 8.94	35.91 ± 20.20	23.73 ± 7.61	26.39 ± 12.32	29.33 ± 10.66	29.21 ± 13.18	30.17 ± 11.18	35.55 ± 8.67
Jun	28.64 ± 26.22	25.73 ± 11.89	25.76 ± 22.55	29.78 ± 5.51	24.19 ± 10.21	27.27 ± 13.23	30.26 ± 5.99	34.81 ± 6.16
Aug	20.70 ± 14.63	23.92 ± 8.45	17.17 ± 12.28	19.17 ± 8.60	12.80 ± 10.59	20.69 ± 8.25	19.62 ± 14.00	12.33 ± 7.50
Oct	19.56 ± 7.09	16.45 ± 7.56	19.05 ± 12.27	17.73 ± 9.94	10.41 ± 6.17	16.30 ± 4.70	18.87 ± 16.43	14.80 ± 10.50
BLADE LENGTH (cm)								
Jan	7.92 ± 2.10	7.47 ± 1.64	9.76 ± 3.65	11.28 ± 2.60	6.48 ± 1.66	9.09 ± 3.13	8.27 ± 2.44	7.56 ± 1.99
Mar	8.58 ± 2.42	9.05 ± 1.39	9.80 ± 3.01	10.34 ± 1.74	6.83 ± 1.94	11.01 ± 3.57	8.23 ± 2.05	7.33 ± 1.60
May	14.66 ± 4.66	15.31 ± 4.04	24.47 ± 5.01	18.57 ± 2.88	13.34 ± 4.23	22.68 ± 3.49	21.07 ± 4.34	13.79 ± 2.99
Jun	19.64 ± 4.18	20.23 ± 4.93	33.77 ± 8.12	24.11 ± 4.62	21.05 ± 3.68	24.61 ± 7.70	17.78 ± 2.83	14.49 ± 3.98
Aug	15.96 ± 3.37	18.92 ± 5.06	25.15 ± 7.13	18.45 ± 4.99	14.87 ± 4.18	31.45 ± 8.35	14.23 ± 4.55	13.11 ± 3.61
Oct	11.47 ± 3.50	16.79 ± 4.82	19.54 ± 7.39	13.81 ± 5.96	11.03 ± 2.26	25.10 ± 5.78	13.35 ± 4.15	9.65 ± 3.11
PRODUCTION (g dry wt/m²/day)								
Jan	0.08 ± 0.07	0.04 ± 0.04	0.08 ± 0.10	0.15 ± 0.15	0.01 ± 0.01	0.00 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
Mar	0.69 ± 0.33	0.54 ± 0.26	0.33 ± 0.26	1.25 ± 0.33	0.06 ± 0.04	0.07 ± 0.07	0.17 ± 0.10	0.14 ± 0.05
May	2.78 ± 1.24	2.94 ± 2.74	2.20 ± 0.91	5.65 ± 2.40	0.51 ± 0.23	1.01 ± 0.63	0.69 ± 0.31	0.60 ± 0.20
Jun	0.76 ± 0.45	0.97 ± 0.57	3.12 ± 3.51	3.63 ± 0.86	0.48 ± 0.22	0.65 ± 0.42	0.45 ± 0.07	0.60 ± 0.25
Aug	0.99 ± 0.76	0.81 ± 0.41	1.44 ± 1.31	1.29 ± 0.84	0.15 ± 0.11	0.56 ± 0.29	0.34 ± 0.31	0.09 ± 0.07
Oct	0.69 ± 0.46	0.50 ± 0.30	0.45 ± 0.34	0.54 ± 0.51	0.06 ± 0.05	0.18 ± 0.10	0.46 ± 1.31	0.06 ± 0.05
PRODUCTION PER SHOOT (mg dry wt/g dry wt/day)								
Jan	0.21 ± 0.19	0.26 ± 0.20	0.30 ± 0.37	0.47 ± 0.49	0.14 ± 0.17	0.07 ± 0.11	0.37 ± 0.36	0.17 ± 0.16
Mar	1.96 ± 0.93	2.54 ± 1.24	1.45 ± 1.15	3.79 ± 0.99	1.12 ± 0.75	1.08 ± 1.14	2.55 ± 1.46	2.13 ± 0.79
May	8.91 ± 3.97	10.90 ± 10.15	7.69 ± 3.17	13.54 ± 5.76	7.69 ± 3.43	12.33 ± 7.66	12.34 ± 5.44	8.72 ± 2.95
Jun	6.71 ± 3.93	6.22 ± 3.69	11.05 ± 12.44	10.92 ± 2.58	6.17 ± 2.79	8.28 ± 5.40	8.09 ± 1.29	6.23 ± 2.64
Aug	2.83 ± 2.16	4.64 ± 2.33	4.54 ± 4.13	4.57 ± 2.97	1.96 ± 1.41	6.61 ± 3.37	3.06 ± 2.88	1.51 ± 1.21
Oct	2.57 ± 1.70	2.97 ± 1.78	2.83 ± 2.14	3.99 ± 3.81	1.33 ± 1.08	4.00 ± 2.10	7.02 ± 19.93	1.09 ± 0.85

Appendix Table C.2. Mean and standard deviations for core parameter analyses for each station, depth and date.

	MUL S	PIN S	PRT S	RIV S	MUL D	PIN D	PRT D	RIV D
A_B								
Jan	0.141 ± 0.052	0.266 ± 0.144	0.249 ± 0.301	0.153 ± 0.037	0.227 ± 0.094	0.702 ± 0.401	0.243 ± 0.209	0.390 ± 0.204
May	0.440 ± 0.105	0.954 ± 0.857	0.465 ± 0.111	0.420 ± 0.199	0.566 ± 0.346	1.516 ± 0.855	0.575 ± 0.272	0.364 ± 0.093
Aug	0.258 ± 0.134	0.243 ± 0.096	0.309 ± 0.082	0.240 ± 0.073	0.228 ± 0.051	0.596 ± 0.304	0.196 ± 0.097	0.187 ± 0.072
Oct	0.177 ± 0.079	0.224 ± 0.073	0.215 ± 0.060	0.215 ± 0.192	0.151 ± 0.060	0.460 ± 0.218	0.108 ± 0.047	0.081 ± 0.045
AG_BG_RATO								
Jan	0.142 ± 0.052	0.267 ± 0.144	0.249 ± 0.301	0.152 ± 0.036	0.228 ± 0.093	0.703 ± 0.402	0.242 ± 0.209	0.390 ± 0.205
May	0.440 ± 0.104	0.953 ± 0.857	0.466 ± 0.111	0.419 ± 0.198	0.565 ± 0.347	1.515 ± 0.856	0.574 ± 0.271	0.363 ± 0.094
Aug	0.259 ± 0.134	0.242 ± 0.096	0.311 ± 0.084	0.240 ± 0.072	0.228 ± 0.051	0.597 ± 0.305	0.196 ± 0.097	0.187 ± 0.071
Oct	0.177 ± 0.080	0.225 ± 0.074	0.216 ± 0.060	0.214 ± 0.192	0.151 ± 0.060	0.460 ± 0.218	0.109 ± 0.047	0.082 ± 0.044
AGC_BIO_M2								
Jan	32.8 ± 11.7	24.1 ± 8.8	39.2 ± 24.8	54.0 ± 13.2	7.7 ± 3.2	26.4 ± 23.2	14.9 ± 15.8	21.3 ± 13.3
May	113.3 ± 18.1	197.3 ± 119.0	112.3 ± 32.7	216.2 ± 70.1	35.9 ± 17.6	57.6 ± 29.1	38.9 ± 15.9	28.6 ± 10.0
Aug	38.3 ± 16.9	28.8 ± 12.9	62.3 ± 19.5	46.3 ± 9.4	15.9 ± 4.2	20.8 ± 5.7	16.5 ± 5.2	9.3 ± 1.9
Oct	31.1 ± 13.1	21.2 ± 6.6	23.2 ± 7.2	20.2 ± 13.1	6.1 ± 2.4	11.4 ± 4.0	7.4 ± 3.1	2.7 ± 1.3
BGC_BIO								
Jan	243.4 ± 88.2	100.2 ± 29.0	233.2 ± 107.5	366.9 ± 125.0	34.6 ± 7.6	41.6 ± 28.3	64.1 ± 33.4	57.0 ± 19.3
May	264.7 ± 49.4	246.5 ± 92.6	251.7 ± 79.2	561.7 ± 189.9	70.9 ± 27.2	43.4 ± 18.5	75.9 ± 28.6	80.8 ± 28.9
Aug	170.8 ± 79.3	120.5 ± 40.0	211.2 ± 74.3	205.0 ± 62.4	71.3 ± 18.6	45.3 ± 28.0	94.0 ± 30.7	56.2 ± 24.2
Oct	189.1 ± 62.6	97.3 ± 20.6	109.1 ± 20.1	122.3 ± 61.3	42.3 ± 16.2	26.9 ± 7.0	69.3 ± 11.0	36.7 ± 10.9
NECWTR								
Jan	0.385 ± 0.240	0.234 ± 0.130	0.249 ± 0.135	0.426 ± 0.173	0.235 ± 0.142	0.690 ± 0.608	0.661 ± 0.846	0.301 ± 0.156
May	0.621 ± 0.450	0.380 ± 0.311	0.337 ± 0.345	0.262 ± 0.158	0.090 ± 0.126	0.135 ± 0.107	0.308 ± 0.190	0.122 ± 0.061
Aug	0.192 ± 0.107	0.403 ± 0.237	0.202 ± 0.131	0.257 ± 0.167	0.221 ± 0.113	0.187 ± 0.076	0.178 ± 0.100	0.102 ± 0.073
Oct	0.110 ± 0.109	0.103 ± 0.097	0.042 ± 0.033	0.096 ± 0.078	0.075 ± 0.068	0.140 ± 0.146	0.079 ± 0.068	0.016 ± 0.013
PROD_PER								
Jan	12.2 ± 3.9	20.2 ± 8.0	16.9 ± 14.0	13.2 ± 2.6	18.1 ± 6.4	38.5 ± 13.4	17.6 ± 13.0	26.7 ± 10.7
May	30.2 ± 5.0	42.5 ± 16.7	31.4 ± 5.9	28.4 ± 9.3	33.6 ± 12.8	56.4 ± 12.9	34.8 ± 11.1	26.4 ± 5.0
Aug	19.8 ± 8.1	19.1 ± 6.7	23.3 ± 5.0	19.1 ± 4.5	18.4 ± 3.3	35.3 ± 12.3	15.9 ± 6.4	15.5 ± 5.0
Oct	14.7 ± 5.7	18.0 ± 4.9	17.5 ± 4.0	16.2 ± 11.0	12.9 ± 4.3	30.2 ± 9.7	9.6 ± 3.6	7.4 ± 3.7
PRODWT								
Jan	0.92 ± 0.46	0.79 ± 0.21	0.57 ± 0.34	1.15 ± 0.40	0.34 ± 0.12	0.99 ± 0.40	0.84 ± 0.64	0.77 ± 0.58
May	3.18 ± 0.75	2.95 ± 1.28	2.88 ± 1.16	3.01 ± 0.98	1.51 ± 0.74	2.38 ± 1.08	2.48 ± 1.38	1.25 ± 0.41
Aug	0.57 ± 0.22	0.73 ± 0.35	1.17 ± 0.58	1.24 ± 0.40	0.65 ± 0.41	0.79 ± 0.42	0.55 ± 0.25	0.44 ± 0.14
Oct	0.54 ± 0.37	0.80 ± 0.24	0.89 ± 0.31	0.88 ± 0.50	0.34 ± 0.15	0.84 ± 0.33	0.42 ± 0.16	0.17 ± 0.05

Appendix Table C.2. Continued.

Page 2

	MUL S	PIN S	PRT S	RIV S	MUL D	PIN D	PRT D	RIV D
RHIZ_DEN								
Jan	0.190 ± 0.054	0.182 ± 0.040	0.180 ± 0.030	0.362 ± 0.165	0.223 ± 0.051	0.176 ± 0.052	0.216 ± 0.032	0.319 ± 0.197
May	0.178 ± 0.059	0.209 ± 0.041	0.217 ± 0.136	0.198 ± 0.042	0.170 ± 0.043	0.174 ± 0.060	0.207 ± 0.029	0.189 ± 0.033
Aug	0.143 ± 0.041	0.194 ± 0.056	0.200 ± 0.052	0.220 ± 0.074	0.189 ± 0.040	0.153 ± 0.031	0.234 ± 0.074	0.179 ± 0.047
Oct	0.155 ± 0.038	0.154 ± 0.031	0.142 ± 0.019	0.190 ± 0.040	0.225 ± 0.126	0.190 ± 0.061	0.186 ± 0.031	0.169 ± 0.028
RHIZ_VOL								
Jan	26.39 ± 14.48	9.79 ± 6.73	12.11 ± 6.89	12.53 ± 8.36	5.04 ± 3.88	6.71 ± 4.93	10.86 ± 5.02	5.17 ± 3.12
May	25.31 ± 8.66	14.80 ± 6.80	16.59 ± 9.91	19.90 ± 8.95	11.96 ± 7.36	5.15 ± 3.61	11.97 ± 6.73	13.05 ± 6.26
Aug	13.03 ± 6.91	7.89 ± 3.41	10.15 ± 7.12	15.41 ± 8.50	8.84 ± 5.09	9.65 ± 5.77	10.74 ± 7.90	10.78 ± 3.95
Oct	15.08 ± 7.23	12.19 ± 7.59	15.40 ± 5.33	15.63 ± 10.46	8.28 ± 4.08	5.91 ± 5.21	12.44 ± 7.24	11.70 ± 4.58
RHIZ_W_L								
Jan	0.044 ± 0.007	0.045 ± 0.010	0.044 ± 0.007	0.090 ± 0.035	0.067 ± 0.018	0.045 ± 0.011	0.061 ± 0.014	0.079 ± 0.036
May	0.049 ± 0.009	0.066 ± 0.021	0.057 ± 0.031	0.086 ± 0.030	0.059 ± 0.018	0.058 ± 0.016	0.072 ± 0.012	0.078 ± 0.018
Aug	0.038 ± 0.008	0.043 ± 0.014	0.044 ± 0.007	0.063 ± 0.016	0.045 ± 0.006	0.044 ± 0.005	0.072 ± 0.017	0.072 ± 0.016
Oct	0.039 ± 0.008	0.039 ± 0.008	0.038 ± 0.006	0.060 ± 0.009	0.065 ± 0.026	0.043 ± 0.010	0.049 ± 0.006	0.064 ± 0.012
ROOTZ_PER								
Jan	59.35 ± 10.84	31.53 ± 13.89	35.30 ± 18.74	42.85 ± 13.67	36.63 ± 15.86	26.40 ± 18.28	50.87 ± 14.73	47.02 ± 14.16
May	39.34 ± 8.05	27.50 ± 18.23	31.93 ± 10.61	35.20 ± 12.51	40.37 ± 10.59	17.18 ± 19.82	27.26 ± 12.89	48.84 ± 7.62
Aug	55.84 ± 10.78	37.85 ± 10.80	27.87 ± 15.74	35.53 ± 12.97	48.07 ± 9.60	11.54 ± 18.97	22.20 ± 22.05	62.75 ± 10.24
Oct	60.08 ± 10.31	36.97 ± 14.84	39.91 ± 7.44	44.52 ± 16.57	59.32 ± 9.80	27.94 ± 13.91	44.03 ± 11.85	70.76 ± 7.40
ROOTZWT								
Jan	4.54 ± 1.80	1.55 ± 1.22	1.78 ± 1.48	3.82 ± 1.79	0.87 ± 0.75	0.99 ± 1.09	2.26 ± 0.89	1.33 ± 0.74
May	4.26 ± 1.44	2.45 ± 1.79	2.87 ± 1.15	3.78 ± 1.46	1.89 ± 0.98	0.60 ± 0.68	2.16 ± 1.32	2.50 ± 1.52
Aug	1.73 ± 0.90	1.40 ± 0.45	1.57 ± 1.09	2.72 ± 1.67	1.62 ± 0.78	0.50 ± 0.92	1.14 ± 1.33	1.84 ± 0.59
Oct	2.15 ± 0.74	1.69 ± 0.86	2.01 ± 0.72	2.86 ± 1.76	1.54 ± 0.59	0.90 ± 0.77	2.25 ± 1.30	2.01 ± 0.92
SCAR_L								
Jan	12.45 ± 1.86	9.75 ± 1.51	8.15 ± 4.82	8.93 ± 1.88	11.61 ± 1.83	5.83 ± 5.20	11.43 ± 1.54	13.05 ± 4.96
May	13.01 ± 2.61	6.94 ± 4.84	5.89 ± 3.41	8.04 ± 4.53	11.45 ± 2.34	6.28 ± 2.61	10.40 ± 14.81	10.70 ± 2.80
Aug	11.27 ± 1.73	8.56 ± 3.56	5.48 ± 6.90	8.47 ± 4.76	9.06 ± 3.85	1.44 ± 3.12	3.53 ± 4.71	12.18 ± 2.83
Oct	10.21 ± 4.54	5.26 ± 5.63	8.35 ± 1.66	6.14 ± 5.46	4.57 ± 6.12	2.19 ± 3.91	8.27 ± 3.50	13.63 ± 2.06
SHOOT_P								
Jan	28.45 ± 8.89	48.26 ± 8.50	47.77 ± 13.25	43.92 ± 11.96	45.31 ± 11.66	35.15 ± 15.98	31.53 ± 8.60	26.31 ± 7.71
May	30.40 ± 9.02	29.98 ± 7.42	36.73 ± 5.88	36.40 ± 6.15	26.01 ± 8.17	26.43 ± 12.03	37.94 ± 9.57	24.79 ± 4.88
Aug	24.38 ± 5.47	43.05 ± 8.89	48.82 ± 14.09	45.34 ± 9.14	33.50 ± 10.70	53.19 ± 13.31	61.89 ± 19.71	21.75 ± 7.92
Oct	25.25 ± 9.66	45.03 ± 12.24	42.55 ± 8.95	39.31 ± 14.72	27.80 ± 5.86	41.87 ± 7.10	46.37 ± 12.03	21.86 ± 6.91

Appendix Table C.2. Continued.

Page 3

	MUL S	PIN S	PRT S	RIV S	MUL D	PIN D	PRT D	RIV D
SHOOTDEN								
Jan	350.8 ± N/A	172.8 ± N/A	280.4 ± N/A	306.8 ± N/A	60.9 ± N/A	64.8 ± N/A	36.0 ± N/A	70.6 ± N/A
May	312.0 ± N/A	269.6 ± N/A	286.4 ± N/A	417.2 ± N/A	66.0 ± N/A	82.0 ± N/A	56.0 ± N/A	68.9 ± N/A
Aug	349.4 ± N/A	174.4 ± N/A	316.8 ± N/A	282.4 ± N/A	76.9 ± N/A	85.0 ± N/A	109.3 ± N/A	57.0 ± N/A
Oct	269.5 ± N/A	168.0 ± N/A	158.4 ± N/A	134.8 ± N/A	44.4 ± N/A	45.6 ± N/A	65.6 ± N/A	54.4 ± N/A
SHOOTWT								
Jan	2.15 ± 1.05	2.02 ± 0.64	2.10 ± 1.13	3.82 ± 1.45	0.92 ± 0.53	1.05 ± 0.72	1.41 ± 0.67	0.73 ± 0.39
May	3.28 ± 1.24	2.30 ± 1.23	3.35 ± 1.41	3.88 ± 0.80	1.38 ± 1.20	1.17 ± 0.75	2.75 ± 1.28	1.18 ± 0.42
Aug	0.80 ± 0.65	1.68 ± 0.81	2.46 ± 1.37	3.05 ± 1.11	1.16 ± 0.65	1.23 ± 0.62	2.04 ± 0.64	0.66 ± 0.40
Oct	0.95 ± 0.68	2.00 ± 0.62	2.07 ± 0.55	2.29 ± 0.78	0.72 ± 0.24	1.24 ± 0.54	2.13 ± 1.11	0.61 ± 0.32