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# CHANGES IN GROWTH AND ABUNDANCE OF SEAGRASSES IN BARBADOS, WEST INDIES

By

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Submitted in partial fulfillment of the requirements for the degree
Doctorate of Philosophy

at

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*this is for my parents, Kees and Rebecca*

*and for my beautiful god daughter, Rhea... may you always find happiness*

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## GENERAL ABSTRACT

The goal of the research was to document and interpret short and long-term changes in growth and abundance of seagrasses (*Thalassia testudinum*, *Syringodium filiforme*) in Barbados. The short-term changes were in response to a 15-month discharge of turbid water into St. Lawrence Bay; the long-term changes were over the 25-year period 1969-1994. To facilitate interpretation of the changes, effects of seasonality and shoot age on *Thalassia* were investigated, and nutrient and light competition between *Thalassia* and *Syringodium* was assessed. Seasonal variation was observed in growth of *Thalassia*, being highest when nutrient availability (leaf nutrient levels) was highest. Effects of shoot age on *Thalassia* leaf growth were investigated in 3 shoot age categories. Most growth variables increased with shoot age, with shoot age explaining more of the variance in younger than older shoot age categories. *Thalassia* abundance and growth decreased significantly during the 15-month discharge event in St. Lawrence Bay, probably through reduced light levels. *Syringodium* abundance increased during the event, probably through increased nutrient availability, suggesting that *Thalassia* may be the more effective nutrient competitor. This may result from the higher belowground to aboveground biomass ratio characteristic of *Thalassia*. In a canopy removal experiment, *Syringodium* inhibited *Thalassia* growth through light competition more than the reverse. This suggests that *Syringodium* is the more effective light competitor, possibly because of its higher aboveground to belowground biomass ratio. *Thalassia* abundance and growth decreased, and *Syringodium* abundance increased, between 1969 and 1994. The impact of a hurricane in 1980 may best explain the *Thalassia* loss, and the *Syringodium* increase may be a response to this loss. The decrease in *Thalassia* growth could result from increased light competition from *Syringodium*, from a long term decrease in coastal water clarity believed to have occurred in Barbados, or perhaps from a younger *Thalassia* shoot age distribution resulting from the hurricane impact.

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# GENERAL INTRODUCTION

Seagrasses are marine angiosperms with extensive root and rhizome systems, dense leaf development and high growth rates. They occur in shallow subtidal areas, being restricted to depths with adequate light penetration and light quality for photosynthesis. They typically grow in unconsolidated sediments, from which they extract most of their required nutrients. Their geographical distribution ranges from the Arctic to the southern tips of Africa and New Zealand. Approximately 60 species of seagrasses comprising 12 genera occur globally. Seven of these genera are tropical in distribution, and 4 occur in the Caribbean, namely *Halodule*, *Halophila*, *Syringodium* and *Thalassia*. Further information on the biology of seagrasses is provided in Appendix A.

Seagrasses are among the most productive of all primary producers, and are the basis of food chains both within and outside of the seagrass community (McRoy and McMillan 1977; Zieman 1983; Hatcher *et al.* 1989). Seagrass beds are important for coastal fisheries. They serve as juvenile and adult habitat for several species that are commercially harvested (e.g. shrimp, lobsters, conch, sea urchins, mullets; Young 1978, Brownell and Stevely 1981, Scheibling and Mladenov 1987, Coles *et al.* 1993, Walker and McComb 1992), as nursery habitat for commercially important reef fish (e.g. groupers, parrotfish, surgeonfish; Ogden 1976, McRoy and Helfferich 1980, Tomascik *et al.* 1997) and as foraging habitat to which adult reef fish routinely migrate (e.g. grunts, snappers, parrotfish, squirrelfish; Zieman *et al.* 1984). Studies have shown that coral reefs near to seagrass beds have larger and more diverse reef fish populations than reefs without nearby beds (Randall 1965; Starck and Davis 1966; Ogden 1972; Salm and Clark 1984). Seagrass beds are also important in physically stabilising the coastal zone. Their dense leaf canopy reduces current velocity near the sediment surface and promotes sedimentation, and the roots and rhizomes bind sediments and limit erosion (Ward *et al.* 1984; Fonseca and Cahalan 1992).

The shallow, nearshore location of seagrass beds makes them vulnerable to land-based pollution and other anthropogenic coastal activities (e.g. dredging, filling and land reclamation, eutrophication, agricultural run-off, industrial pollution; Zieman 1975a, Thorhaug and Marcus 1987, Fortes 1988, Pulich and White 1991, Lapointe *et al.* 1994). Local declines in seagrass abundance have been documented in many countries (e.g. Florida, USA: Robblee *et al.* 1991, Durako 1994, Thayer *et al.* 1994, Fletcher and Fletcher 1995, Tomasko *et al.* 1996; Australia: Cambridge *et al.* 1986, Shepherd *et al.* 1989, Walker and McComb 1992; Netherlands: den Hartog and Polderman 1975; Mediterranean: Marba *et al.* 1996). Natural factors also contribute to seagrass decline. These include disease (den Hartog and Polderman 1975; Short *et al.* 1988; Durako and Kuss 1994; Vergeer and den Hartog 1994), severe storm events (Poiner *et al.* 1989; van Tussenbroek 1994; Preen *et al.* 1995), overgrazing (Thayer *et al.* 1984; Valentine and Heck 1991), changes in sea temperature (Bulthuis 1987; Masini and Manning 1997), and changes in salinity (Zieman *et al.* 1999). Many of these factors may be exacerbated by human activities. For example, hypersalinity in Florida Bay was caused by a regional drought aggravated by the diversion of freshwater for flood control, agriculture and urban water use (Zieman *et al.* 1999); and the frequency and severity of storm events may be increasing in response to global warming (Fortes 1995; Landsea 1999).

There have been few seagrass studies in the eastern Caribbean, defined here as Barbados and the islands in the Lesser Antilles chain. The principal published accounts are those of Patriquin (1971, 1972, 1973, 1975). Patriquin's work was conducted in 1969 at 2 sites (Bath, St. Lawrence) in Barbados, and at several locations around Carriacou, and focused on abundance and growth of the dominant seagrass *Thalassia testudinum*. His work, along with that of Zieman (1974), was among the first to study *Thalassia* growth and to use plastochron interval (the time between production of successive leaves on a shoot) as a tool for ageing *Thalassia* shoots. This technique has subsequently been the basis for numerous demographic studies of *Thalassia* (e.g. Duarte *et al.* 1994). Patriquin's work emphasised the physically dynamic nature of *Thalassia* beds (Patriquin 1975), and indicated that *Thalassia* in Barbados was nutrient limited (Patriquin 1971). He identified nitrogen as the limiting nutrient, and demonstrated that nitrogen-fixation was a significant source of nitrogen for *Thalassia* (Patriquin and Knowles 1972). Studies of anthropogenic impacts on seagrass growth and abundance have not been conducted in the eastern Caribbean. However, there is a widespread qualitative perception that seagrass abundance is declining in the region, and nearshore coral reefs are known to have deteriorated in recent decades in response to deteriorating water quality and to a disease event which decimated populations of an important coral reef grazer (Tomascik and Sander 1987; Lessios 1988; Wittenberg and Hunte 1992; Allard 1993).

The overall goal of my research was to document and interpret short-term and long-term changes in growth and abundance of seagrasses in Barbados, and through this to contribute to our understanding of requirements for effective conservation and monitoring. The approach used was to take advantage of two specific opportunities. The first was the existence of an historical data set created by Patriquin's work in 1969. The same seagrass sites surveyed by Patriquin were revisited in 1994, and the same growth and abundance variables remeasured. This comparison, supplemented by an analysis of aerial photographs, allowed seagrass changes which have occurred over the 25-year period 1969 to 1994 to be documented. The study sites differ in their exposure to anthropogenic and natural disturbances, and therefore provide the opportunity to comment on long-term changes detected in this context (see Chapter 5). This 25-year comparison is one of only a few studies anywhere that have assessed seagrass changes over an extended time period (but see Birch and Birch 1984 in Australia; Fletcher and Fletcher 1995 in Central Florida; Fourqurean and Robblee 1999, Hall *et al.* 1999, and Zieman *et al.* 1999 in Florida Bay; and note the recent establishment of a monitoring program on selected seagrass variables in Barbados by the Caribbean Coastal Marine Productivity Program (CARICOMP); Parker and Oxenford 1998).

The second opportunity for assessing seagrass changes arose through the occurrence of a planned anthropogenic disturbance that lasted for the 15-month period between March 1996 and May 1997. The disturbance resulted from the construction of a sewage treatment facility near the periphery of a mangrove swamp inland of a seagrass site at St. Lawrence, Barbados. The construction site had to be drained, and the water was pumped into an adjacent mangrove pond, and discharged via a sluice gate into St. Lawrence Bay. This situation created an unique opportunity to investigate effects of water quality changes on seagrasses as the changes were occurring (see Chapter 3).

Interpretation of seagrass changes in response to anthropogenic and natural disturbances is complicated by the fact that there are many other biological processes which may cause variation in seagrass growth and abundance. Such effects should be known and considered in attempts to interpret temporal changes and spatial differences in seagrass growth and abundance. Possible seasonal effects on growth and abundance of the dominant seagrass *Thalassia testudinum* in Barbados are investigated in Chapter 1, and effects of shoot age on *Thalassia* growth are explored in Chapter 2.

Anthropogenic impacts on a seagrass species may not occur directly, but may be mediated through competitive interactions with other species. In the Caribbean, *Thalassia testudinum* is the climax species in seagrass bed development, and is typically the most common species. Changes in *Thalassia* growth and abundance are therefore the principal focus of the present research. The general successional sequence in the Caribbean is colonisation of substrata by rhizophytic green macroalgae, followed by the seagrasses *Halodule wrightii* and/or *Syringodium filiforme*, and ending with *T. testudinum* (den Hartog 1971; Zieman 1976; Williams 1987, 1990). It has been suggested that disturbances can cause reversal of the seral development of seagrass beds, and Lapointe *et al.* (1994) and Fourqurean *et al.* 1995 have documented increased abundance of *Halodule* and decreased abundance of *Thalassia* in response to eutrophication. Reversal of seagrass seral development from *Thalassia* to *Syringodium* has not been reported. Given the potential for competitive effects between seagrass species, changes in both *Thalassia* and *Syringodium* were recorded in both the 25-year survey (Chapter 5) and the 15-month assessment of responses to a specific disturbance event (Chapter 3). Interpretation of such changes will clearly be facilitated by improved understanding of competitive interactions between *Thalassia* and *Syringodium*, and these are investigated in Chapter 4.

The sequence in which information is presented in this study is: seasonal effects on *Thalassia* in Chapter 1; effects of shoot age on *Thalassia* growth in Chapter 2; effects of the 15-month anthropogenic disturbance event on *Thalassia* and *Syringodium* in Chapter 3; an investigation of competitive interactions between *Thalassia* and *Syringodium* in Chapter 4; and documentation and interpretation of long-term (25-year) changes in *Thalassia* and *Syringodium* in Chapter 5.

# CHAPTER 1 SEASONAL OBSERVATIONS OF ABUNDANCE, LEAF GROWTH AND SHOOT DEMOGRAPHY OF THE SEAGRASS *THALASSIA TESTUDINUM* IN BARBADOS

## 1.1 ABSTRACT

Seasonal observations of abundance, leaf growth, shoot recruitment and shoot mortality of *Thalassia testudinum* were recorded at two sites (St. Lawrence; Bath) in Barbados, and seasonal variation in selected environmental variables (salinity, water temperature, rainfall, air temperature, daylength, hours of sunlight, leaf nutrient levels as an indicator of coastal nutrient levels, and abundance of *Syringodium filiforme* as a biotic environmental factor) were documented. There was only modest seasonal variation in air temperature, water temperature, salinity and daylength, and no clear seasonal trend in hours of sunlight. There was strong seasonal variation in rainfall, with most rain occurring between June and November, and significant seasonal variation in nutrient levels (total phosphorous, total nitrogen) in *Thalassia* leaves, with levels being generally highest when rain-driven land-based discharge to the coastal zone would be highest. Plastochron interval (rate of leaf production), leaf growth rate and relative leaf growth rate were the leaf growth variables showing most seasonal variation, with rates being highest when nutrient availability, as indicated by leaf nutrient levels, was highest. This suggests that seasonal variation in *Thalassia* leaf growth may be driven by seasonal variation in nutrient availability. In months when nutrients were most limiting, as indicated by C:P and C:N ratios, N:P ratios were highest, suggesting that phosphorous was more limiting than nitrogen. In 1969, *Thalassia* in Barbados was considered to be primarily nitrogen-limited. This raises the possibility that the heavy nitrogen loading of the coastal zone which has occurred over the past 3 decades has driven the *Thalassia* systems in Barbados from primarily nitrogen limitation to primarily phosphorous limitation. Seasonal variation in *Thalassia* shoot recruitment appeared to be bimodal, with peaks in fall (September-November) and spring (March-April), suggesting that

recruitment seasonality is not driven by seasonality in nutrient availability. Shoot mortality rates were highest around September-November and April-May, and monthly mortality was positively correlated with monthly recruitment. This suggests that *Thalassia* may be close to a shoot density carrying capacity, and is consistent with the observation that seasonal variation in shoot density was weak (St. Lawrence) or negligible (Bath) at the Barbados study sites.

## 1.2 INTRODUCTION

Several studies have documented seasonal variation in abundance and growth of temperate seagrasses, particularly *Zostera marina*, *Z. noltii* and *Posidonia oceanica*, with abundance and growth being highest in summer months (reviewed by Duarte 1989). The consensus is that seasonal variation is primarily driven by variation in light and temperature (e.g. Sand-Jensen 1975; Jacobs *et al.* 1982; Philipps *et al.* 1983; Wium-Andersen and Borum 1984; Kentula and McIntire 1986; Olesen and Sand-Jensen 1994; Alcoverro *et al.* 1995; Philippart 1995; Marba *et al.* 1996; Ibarro-Obando *et al.* 1997; Laugier *et al.* 1999). Seasonal variation in leaf nutrient content of temperate seagrasses has less often been studied, but appears to be lowest when biomass increases are highest (Perez-Llorens and Niell 1993). The leaf nutrient variation is therefore viewed as a consequence of growth variation, with utilisation being faster than uptake in summer months; and nutrient availability is not seen as a limiting factor driving seasonal variation in growth (Perez-Llorens and Niell 1993). The seasonal variation in shoot demography that may underlie abundance variation has been studied less often than growth variation. Vermaat and Verhagen (1996) conclude that seasonal biomass variation in *Zostera noltii* is primarily driven by variation in shoot density rather than shoot size or leaf area, but Laugier *et al.* (1999) suggest that the relative contributions of shoot density and shoot size to seasonal biomass variation in *Z. noltii* and *Z. marina* is dependent on the degree of habitat exposure to wave energy. Duarte *et al.* (1994) refer to several studies of temperate seagrass demography and conclude that shoot recruitment is markedly seasonal, with most recruitment occurring in spring.

Seasonal variation in seagrass species with subtropical and tropical distributions has also received some attention. *Thalassia testudinum* is the dominant seagrass species in the Caribbean and Gulf of Mexico, and is distributed throughout the tropical and subtropical Atlantic (den Hartog 1970; Buesa 1974). A number of studies have shown seasonal variation in leaf growth, biomass and productivity of *T. testudinum* in subtropical areas such as Florida (Zieman 1975b; Dawes and Lawrence 1980; Barber and Behrens 1985; Tomasko and Dawes

1990; Dawes *et al.* 1995; Durako 1995; Tomasko *et al.* 1996; Gacia 1999). As with the temperate studies, seasonal variation in growth and abundance variables in subtropical areas is primarily driven by temperature and light with values being highest in summer months (Perez *et al.* 1991; Perez and Romero 1992). Short *et al.* (1993) and Perez and Romero (1994) support this contention, but suggest that the high growth rates characteristic of the summer may reduce nutrient tissue concentrations to the point where the latter set upper limits to summer growth. Seasonal variation in demographic characteristics of seagrasses in subtropical areas has rarely been studied (but see Zieman 1975b and Durako 1994 for seasonal variation in shoot recruitment of *T. testudinum* in Florida, and Kaldy *et al.* 1999 for demographic characteristics of *T. testudinum* in Texas). The only study to report seasonal variation in *T. testudinum* variables in tropical areas is that of van Tussenbroek (1995,1998) for the tropical Mexican Caribbean. Leaf growth, leaf initiation, biomass and primary production were shown to be highest in summer and lowest in winter, and leaf growth and primary production were significantly correlated with water temperature and/or hours of daylight. By contrast, Buesa (1974,1975) detected no seasonal effects on leaf growth and biomass of *T. testudinum* in Cuba, and Greenway (1974) reported no seasonal variation in leaf growth rates in Jamaica. There have been no studies of seasonal variation in demographic characteristics or tissue nutrient concentrations of *T. testudinum* in tropical areas. It is important to note that, although seasonal variation in temperature and light is expected to be small in tropical areas, there is substantial seasonal variation in rainfall. Seagrasses in tropical areas are typically considered to be nutrient-limited (Lapointe *et al.* 1990; Short *et al.* 1990), and rainfall may influence nutrient input to the coastal zone. McMahon and Walker (1998) have shown significant seasonal variation of input of water-borne nutrients into Geographe Bay, Australia, and significant seasonal responses of shoot nutrient concentrations of the seagrass *Posidonia sinuosa* in the Bay; and Lanyon and Marsh (1995) showed that standing crop of several seagrass species in Townsville, Australia was lowest in the dry season and highest in the wet.

Apart from improving our understanding of seagrass systems in tropical areas, an important rationale for seasonality studies is their value in facilitating the interpretation of long-term trends in seagrass growth and abundance. Throughout its geographical range, *Thalassia testudinum* is important as habitat for coastal biota, in coastal fisheries and in coastline stabilisation, and the perception that growth and abundance of *T. testudinum* may be declining at many locations is cause for concern (Fletcher and Fletcher 1995; Fonseca *et al.* 1998). Accurate interpretation of historical data sets detecting such trends requires knowledge of whether there is seasonal variation in the growth and abundance variables that indicate the trends. In the absence of this, historical data sets will only yield valid indications of long-term trends if the data sets were collected at the same time each year over the time period under survey (see Chapter 5 for changes in abundance and growth of *T. testudinum* in the eastern Caribbean over a 25-year period). Knowledge of seasonal variation at specific locations will be required for appropriate design of monitoring programs established to assess long-term changes in *T. testudinum* abundance and growth.

The objectives of this Chapter are (1) to document seasonal observations of abundance, leaf growth and shoot demography (shoot recruitment and mortality) of *Thalassia testudinum* at 2 sites in Barbados; (2) to document seasonal variation in selected environmental variables at the study sites; and (3) to comment on whether changes observed in the *Thalassia* variables could be a response to seasonal variation in the environmental variables.

## 1.3 METHODS

### 1.3.1 Study Sites

The study was conducted at 2 sites, St. Lawrence and Bath, in Barbados, West Indies (Figure 1.1). The St. Lawrence study site is situated on the south coast of Barbados (Figure 1.1). It consists of a shallow, sandy lagoon adjacent to a mangrove swamp, and is protected offshore by a coral rubble barrier. A narrow drainage channel periodically discharges the water from the swamp via a sluice gate into the nearshore marine environment, but most land-based water entering the coastal zone in the area does so as sub-surface ground water discharge. The coastal and inland areas surrounding the site, and surrounding the inland catchment area discharging at the site, are heavily developed and densely populated. Mean low water depth of the seagrass stands at the site is less than 1 m. Wave action within the lagoon is moderate relative to the Bath study site.

The Bath study site is situated on the east (windward) coast of Barbados (Figure 1.1). Although some protection is provided by a shelf of bedrock and a series of large rocks which lie 200 m offshore, wave action is typically strong and conditions are generally turbulent in the area (Patriquin 1971). There are 4 main substrate types at Bath, namely, cobble framework, cobble sand, *Porites* (coral) rubble flats, and sand (Patriquin 1975). The *Thalassia* beds occur inshore and in the lee of the shelf and large rocks. Mean low water depth of the seagrass stands is approximately 1.5 m. Unlike St. Lawrence, there is little residential and urban development at Bath, and the coastal and inland areas remain lightly populated. However, there is extensive agriculture of sugar cane and other crops in the surrounding area. Land-based water enters the coastal zone in the area as surface run-off and as ground water discharge.

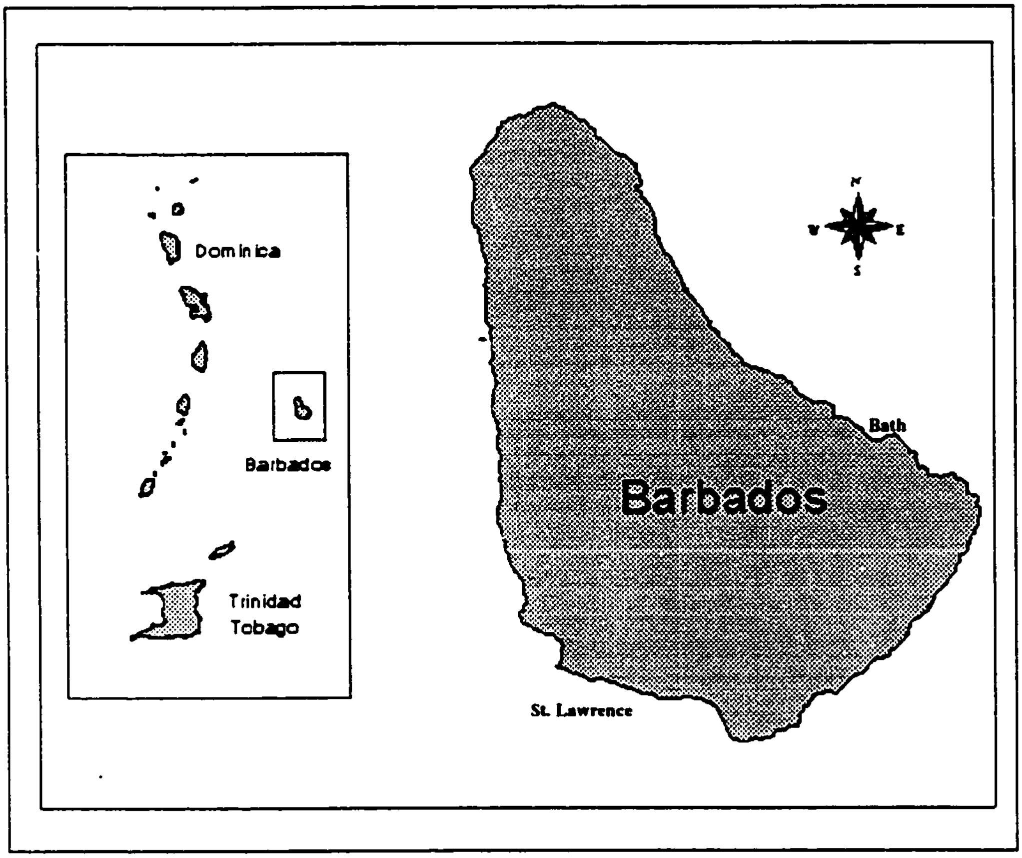


**Figure 1.1.** The locations of Barbados in the eastern Caribbean and of the St. Lawrence and Bath study sites.

## 1.3.2 Seasonal Observations of Abundance and Leaf Growth

### 1.3.2.1 *Sampling Times and Locations*

*Thalassia* abundance and leaf growth data were collected within 3 sampling periods (February, June, October) over a 2-year period (1998-1999) at 8 sites at St. Lawrence; and in the same sampling periods over a 1-year period (1999) at 10 sites at Bath. Each of the 18 study sites consisted of a permanently established 1 $m^2$ area. On each sampling occasion, a 25 cm x 25 cm (0.0625 $m^2$) quadrat was randomly selected in each study site, and the abundance and leaf growth variables were measured using all shoots in the quadrat. However, to achieve a balanced statistical design, the measurements from 10 randomly selected shoots were used for all shoot-specific variables (average leaf growth rate per shoot, relative leaf growth rate per shoot, maximum leaf length, leaf width, leaves per shoot). The decision to measure shoots within 25 cm x 25 cm quadrats was made following *a priori* sampling which indicated no difference in sample variances between shoots randomly selected within the quadrats and shoots randomly selected across the study area.

### 1.3.2.2 *Measurement of Abundance and Growth*

*Thalassia* abundance was measured as shoot density, areal coverage and leaf biomass. Shoot density was measured *in situ* as the number of shoots per 25 cm x 25 cm quadrat, and expressed as the number of shoots per $m^2$. Areal coverage was measured as the total area of leaf material (leaf length x leaf width, summed for all leaves) harvested at substrate level from each 25 cm x 25 cm quadrat, and was expressed as $cm^2$ leaf • $m^{-2}$ substrate. Leaf biomass was measured as dry weight of unepiphytised leaf tissue from all shoots harvested from each 25 cm x 25 cm quadrat, and was expressed as g DW $m^{-2}$. Prior to measuring leaf biomass, calcareous epiphytes were removed by rinsing leaves in 5 % phosphoric acid and gently scraping off any remaining carbonate material. Dry weights were obtained by drying leaves at 70 °C for 24 h or until constant biomass was reached.

*Thalassia* leaf growth was measured as average leaf growth rate per shoot, relative leaf growth rate per shoot, leaf productivity, specific leaf productivity rate, maximum leaf length, leaf width, leaves per shoot and plastochron interval. Average leaf growth rate per shoot, relative leaf growth rate per shoot and leaf productivity were measured by punching a hole at the base of each leaf on all shoots in each 25 cm x 25 cm quadrat, and harvesting all marked shoots, with leaves intact, 8-12 days following marking. Average leaf growth rate per shoot (cm $d^{-1}$) was measured as the summed length of new leaf material produced over the growth period, divided by the number of leaves on the shoot. Relative leaf growth rate per shoot (cm new tissue • $cm^{-1}$ old tissue • $d^{-1}$) was measured for each shoot as the summed length of new leaf tissue produced over the growth period divided by the length of existing (old) leaf tissue. Leaf productivity (g DW $m^{-2}$ $d^{-1}$) was measured as the dry weight of new leaf material produced over the growth period. Specific leaf productivity rate (mg $g^{-1}$ DW $d^{-1}$) was measured as the dry weight of new leaf tissue produced over the growth period divided by the dry weight of existing (old) leaf tissue. Maximum leaf length (cm) was measured as the longest leaf on a shoot for the 10 shoots selected in each quadrat; leaf width (cm) was measured using the second youngest leaf on each shoot for the 10 shoots selected in each quadrat; and leaves per shoot was measured as the number of leaves on each shoot for the 10 shoots selected in each quadrat. Plastochron interval (PI; d) is the time between successive leaf production on a shoot. For each quadrat, PI was measured as the number of marked shoots multiplied by the time between marking and harvesting, and divided by the number of marked shoots which had produced new leaves (Patriquin 1973; Brouns 1985). Note that plastochron interval is more correctly termed phyllochron interval (see Wilhelm and McMaster 1995), but is here referred to as plastochron interval for consistency with other seagrass studies.

### 1.3.2.3 *Data Analysis*

Data were tested for normality using a one-way Kolmogorov-Smirnov test, and for homogeneity of variance using Levene's test, and were natural log transformed where necessary for parametric statistical analyses. Only relative leaf growth rate, specific leaf productivity rate, leaf length and leaf width required transformation prior to parametric analysis. Seasonal differences in average leaf growth rate, relative leaf growth rate, leaf length, leaf width, and leaves per shoot were analysed using nested two-way analyses of variance for Bath, and nested three-way analyses of variance for St. Lawrence. For Bath, season was treated as a fixed factor and site as a random factor nested within season. For St. Lawrence, year and season were fixed factors, with site as a random factor nested within year x season. Type III rather than Type I sums of squares were used to calculate F-values, and significant between season differences at Bath, and significant between year and between season differences at St. Lawrence, were compared using Tukey's HSD test. When no significant differences were detected for nested factors, *post hoc* pooling of nested factor and residual error terms was done to increase the power of the test for detecting differences between season.

Seasonal differences in leaf PI, leaf productivity, specific leaf productivity rate, leaf biomass, shoot density and areal coverage were analysed using three-way analyses of variance for St. Lawrence and two-way analyses of variance for Bath, based on a randomised block design, with site as the blocked factor. Significant differences in season were compared using Tukey's HSD test.

### 1.3.3 Seasonal Observations of Shoot Recruitment and Shoot Mortality

#### 1.3.3.1 *Sampling Times, Locations and Measurements*

Two field studies were conducted. The first provided data on both shoot recruitment and shoot mortality; the second provided data on shoot mortality alone. In the first study, shoot recruitment and shoot mortality were monitored daily over a 1-year period (August 1997 to August 1998) in ten 25 cm x 25 cm quadrats, each randomly placed and permanently fixed in each of the 10 largest seagrass stands in St. Lawrence Bay. To monitor recruitment, each shoot within each quadrat, and new shoots recruiting to the quadrat, were individually tagged. The daily data were pooled to provide the monthly recruitment rate to each quadrat. Shoot recruitment is defined as the emergence of a shoot. Monthly recruitment rate is expressed as the number of new shoots emerging in the quadrats in a month / number of shoots present in the quadrats in that month. To monitor mortality, each of the shoots present in each quadrat at the start of the study, and tagged for the recruitment study, was monitored daily, and the number dying were pooled to provide a monthly mortality in each quadrat. Mortality is expressed as monthly mortality rate, i.e. number of shoots dying in the quadrats in a month / number of shoots present in the quadrats in that month. Since the death of new shoots recruiting to the quadrats during the study were not included in the mortality estimates, this study provided information on seasonal variation in mortality of "mature" shoots (see second field study below).

In the second study, new shoots were randomly selected from 10 locations in close proximity to the 10 permanently located quadrats used in the first field study. They were individually tagged on the day of their emergence and followed for 1 year (August 1997 to August 1998). A total of 151 new shoots were selected and tagged during the study. Mortality of the tagged shoots was assessed every second day over the 1-year period. The number of shoots dying was summed to give monthly mortality data, and mortality was expressed as monthly mortality rate, i.e. number of shoots dying in the month / number of shoots being monitored in that month. This study allowed seasonal variation in mortality to be quantified for young shoots, i.e. shoots less than 1 year old.

#### 1.3.3.2 *Data Analysis*

Monthly differences in shoot recruitment and mortality were analysed using a Friedman two-way analysis of variance, based on a randomised block design. Relationships between monthly shoot recruitment and monthly shoot mortality were determined using Spearman's Rank Correlations.

### 1.3.4 Seasonal Variation in Environmental Variables

The physical environmental variables measured were salinity, water temperature, rainfall, air temperature, daylength and hours of sunlight. Nutrient (C, N, P) concentrations in *Thalassia* leaf tissues were used as an index of coastal nutrient levels (see Short *et al.* 1993 for contention that leaf nutrient tissue concentrations are a more reliable index of nutrient availability than water column nutrient values). *Syringodium filiforme* abundance was measured as a biotic factor that may influence *Thalassia* growth and abundance.

#### 1.3.4.1 *Sampling Times, Locations and Measurements*

Salinity (using an Atago hand-held refractometer) and water temperature (using a standard laboratory thermometer) were measured weekly at St. Lawrence between 1993 and 1999 as part of a CARICOMP monitoring program implemented in Barbados by Bellairs Research Institute. Measurements (1 per sampling occasion) were taken between 10 am and 2 pm 0.5 m below the water surface. Daily measurements of air temperature (mean daily °C), daylength, hours of sunshine and rainfall (mm $d^{-1}$) were also obtained between 1993 and 1999 from the Caribbean Meteorological Institute's monitoring station nearest to the 2 study sites (Grantley Adams International Airport).

Data on *Thalassia* leaf tissue nutrient concentrations were obtained in the 3 sampling periods used for assessment of abundance and growth (February, June, October) over a 1-year period (1999) at the 8 St. Lawrence sites and at 8 of the 10 Bath sites (Section 1.2.2). On each sampling occasion, samples of green, unepiphytised *Thalassia* leaf tissue were collected and rinsed in fresh water to remove adherent epibionts and sediments. The leaves were then dried at 70° C for 24 hours or until a constant weight was reached. The dried leaves were ground to a fine powder using an electric grinder to homogenise the sample. The samples were stored in Nalgene sample vials and frozen until analysis. Total carbon and total nitrogen content was determined for duplicate subsamples of each sample using a Fisons EA-1108 CHN-O analyser at the University of Miami. Total phosphorous content was determined by Philip Analytical Services Inc. (Canada) using colorimetry following hot acid digestion.

*Syringodium* abundance was measured as shoot density in the 3 sampling periods (February, June, October) over a 2-year period (1998-99) at 6 of the 8 St. Lawrence sites, and as shoot density and biomass in the same sampling periods over a 1-year period (1999) at 9 of the 10 Bath sites. The method for measuring *Syringodium* shoot density was as described for *Thalassia* shoot density (see Section 1.3.2.2).

#### 1.3.4.2 *Data Analysis*

Differences in monthly mean salinity, water temperature, rainfall, air temperature and hours of sunlight, between 1999 data and average monthly values for the 1993-98 data sets, were compared using Wilcoxon Paired-Sample Tests to determine whether values in 1999 were typical in relation to the 1993-98 data sets. Seasonal differences in leaf tissue nutrient concentrations were analysed using two-way analyses of variance, based on a randomised block design, with site as the blocked factor; significant differences between time periods were then compared using Tukey's HSD tests. Seasonal differences in *Syringodium* abundance were analysed using a three-way analysis of variance for St. Lawrence, and a two-way analysis of variance for Bath, based on a randomised block design, with site as the blocked factor; significant differences between time periods were then compared using Tukey's HSD tests.

## 1.4 RESULTS

### 1.4.1 Seasonal Changes in Abundance and Leaf Growth

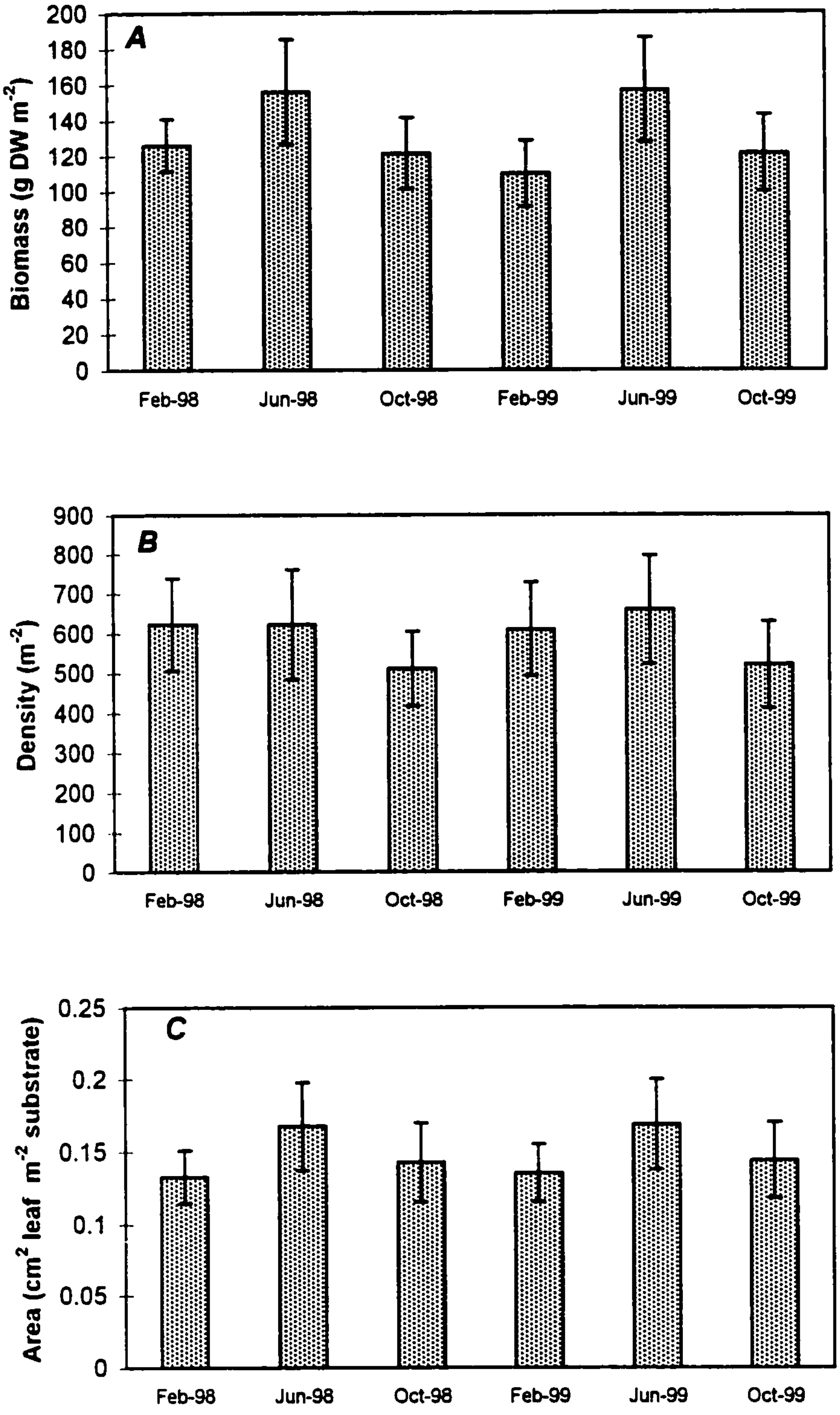
#### 1.4.1.1 *Abundance*

At St. Lawrence, there was a significant effect of season on leaf biomass (Figure 1.2A), and a weak effect of season on shoot density (Figure 1.2B) and on areal coverage (Figure 1.2C). The 3 abundance variables tended to be highest in June; for leaf biomass, the difference between June (highest values) and October (lowest values) was statistically significant (Tukey's HSD test; q=34.89, P<0.05). There was no effect of year and no significant interaction effect between year and season for any of the 3 abundance variables at St. Lawrence (Figures 1.2A-C).

At Bath, there was again a significant effect of season on leaf biomass (Figure 1.3A), a weak effect of season on areal coverage (Figure 1.3C), but no effect of season on shoot density (Figure 1.3B). For leaf biomass, values were significantly lower in October than in February and June (Figure 1.3A; Tukey's HSD test; October<February, q=36.83, P<0.01; October<June, q=37.03, P<0.01).

#### 1.4.1.2 *Leaf Growth*

At St. Lawrence, there was a significant effect of season on plastochron interval (Figure 1.4A) and relative leaf growth rate (Figure 1.4B), a weak effect of season on average leaf growth rate (Figure 1.4C), but no effect of season on leaf length (Figure 1.4D), leaf width (Figure 1.4E), leaves per shoot (Figure 1.4F), leaf productivity (Figure 1.4G) or specific leaf productivity rate (Figure 1.4H). For plastochron interval, values were lowest in October (Figure 1.4A; Tukey's HSD test; October<February, q=3.48, P<0.05; October<June, q=4.51,

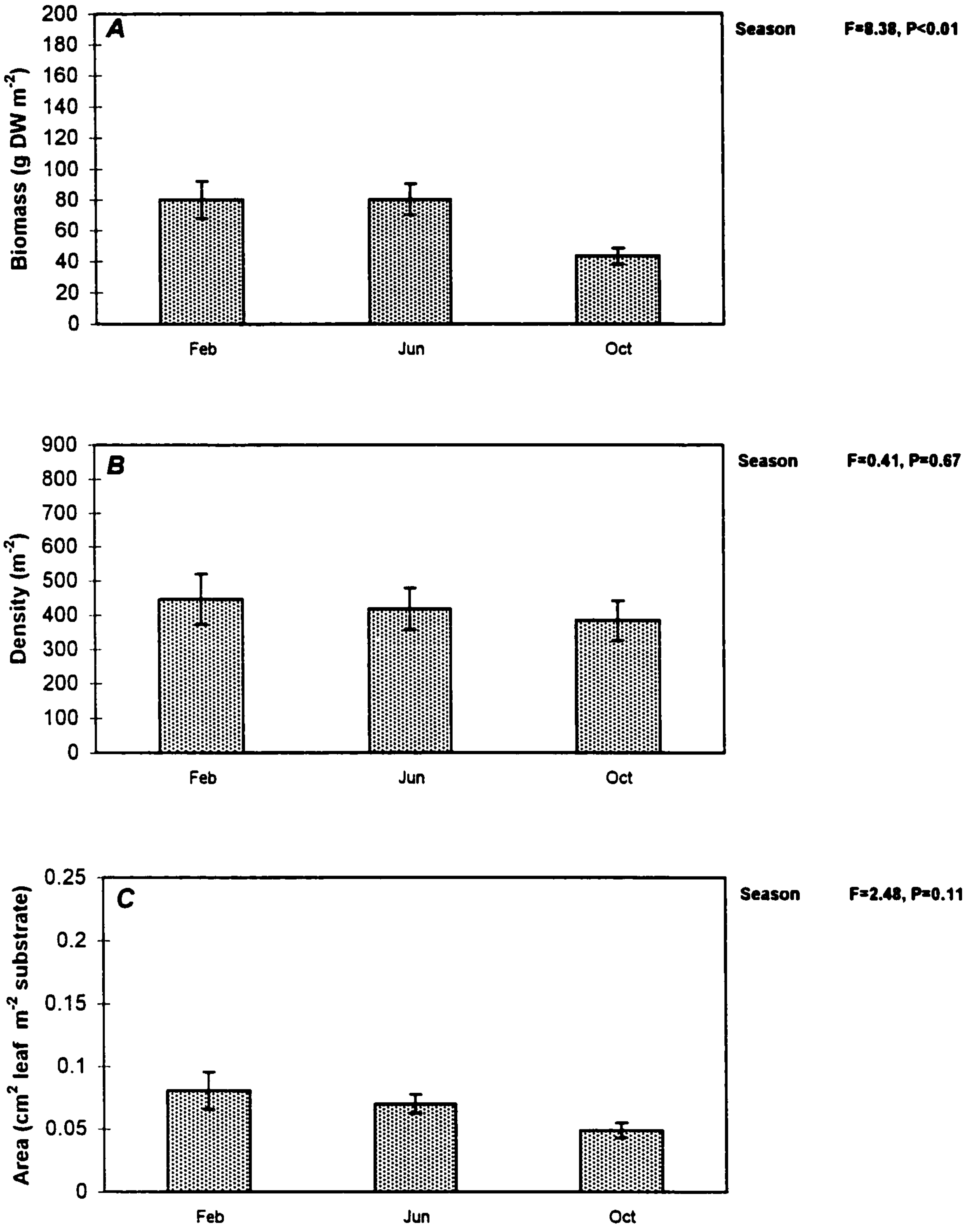


| | |
|---|---|
| **Season** | **F=3.89, P<0.05** |
| **Year** | **F=0.01, P=0.91** |
| **Year*Season** | **F=0.01, P=0.99** |

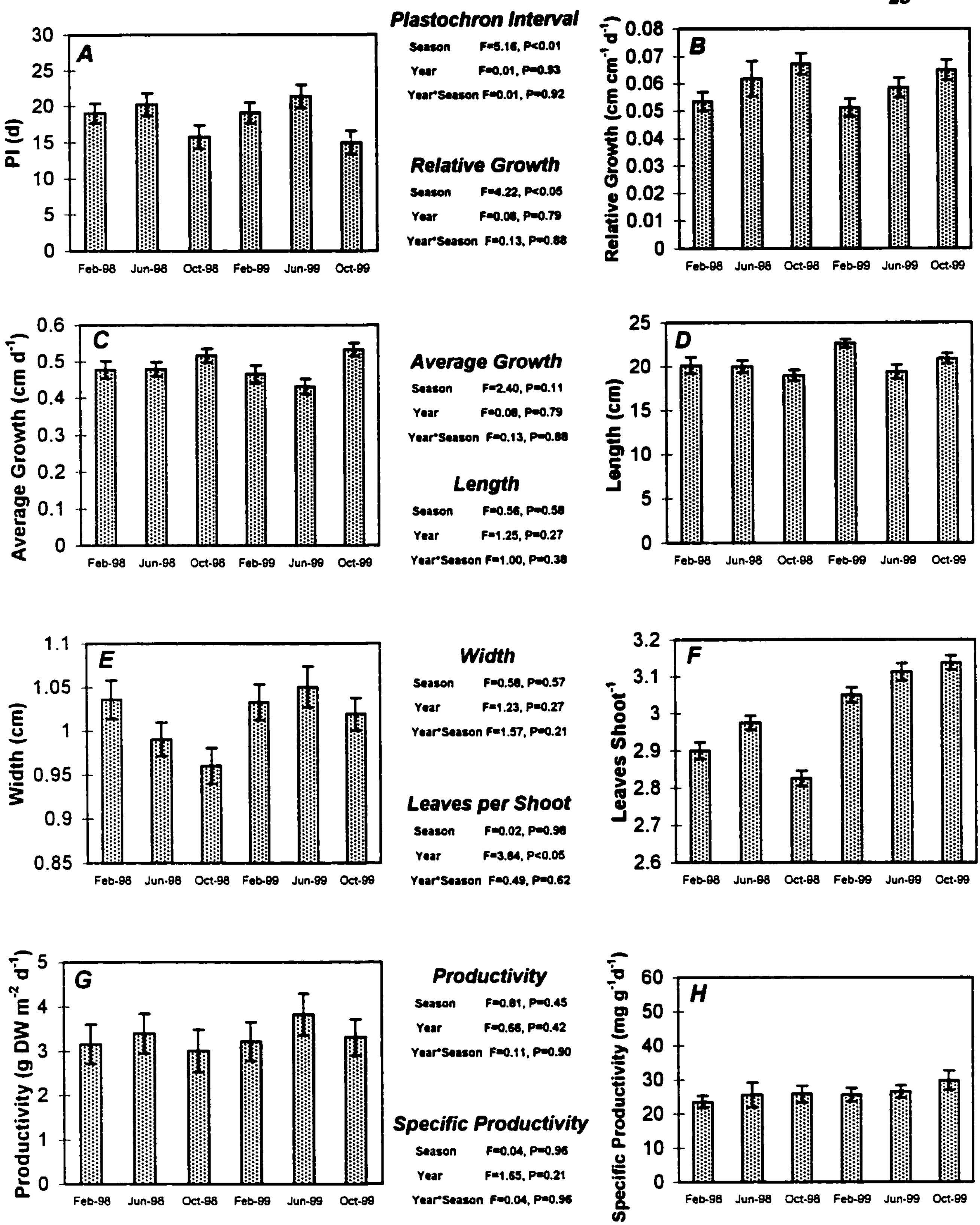
| | |
|---|---|
| **Season** | **F=2.40, P=0.10** |
| **Year** | **F=0.03, P=0.86** |
| **Year*Season** | **F=0.02, P=0.98** |

| | |
|---|---|
| **Season** | **F=2.36, P=0.11** |
| **Year** | **F=0.02, P=0.89** |
| **Year*Season** | **F=0.01, P=0.99** |

Figures 1.2A-C. Seasonal variation in *Thalassia* abundance at St. Lawrence. *(A)* Leaf Biomass, *(B)* Shoot Density, *(C)* Areal Coverage. Values represent means ± SE (N=8). ANOVA results presented.



**Figures 1.3A-C. Seasonal variation in *Thalassia* abundance at Bath. *(A)* Leaf Biomass, *(B)* Shoot Density, *(C)* Areal Coverage. Values represent means ± SE (N=10). ANOVA results presented.**



***Plastochron Interval***

| | |
|---|---|
| Season | F=5.16, P<0.01 |
| Year | F=0.01, P=0.93 |
| Year*Season | F=0.01, P=0.92 |

***Relative Growth***

| | |
|---|---|
| Season | F=4.22, P<0.05 |
| Year | F=0.08, P=0.79 |
| Year*Season | F=0.13, P=0.88 |

***Average Growth***

| | |
|---|---|
| Season | F=2.40, P=0.11 |
| Year | F=0.08, P=0.79 |
| Year*Season | F=0.13, P=0.88 |

***Length***

| | |
|---|---|
| Season | F=0.56, P=0.58 |
| Year | F=1.25, P=0.27 |
| Year*Season | F=1.00, P=0.38 |

***Width***

| | |
|---|---|
| Season | F=0.58, P=0.57 |
| Year | F=1.23, P=0.27 |
| Year*Season | F=1.57, P=0.21 |

***Leaves per Shoot***

| | |
|---|---|
| Season | F=0.02, P=0.98 |
| Year | F=3.84, P<0.05 |
| Year*Season | F=0.49, P=0.62 |

***Productivity***

| | |
|---|---|
| Season | F=0.81, P=0.45 |
| Year | F=0.66, P=0.42 |
| Year*Season | F=0.11, P=0.90 |

***Specific Productivity***

| | |
|---|---|
| Season | F=0.04, P=0.96 |
| Year | F=1.65, P=0.21 |
| Year*Season | F=0.04, P=0.96 |

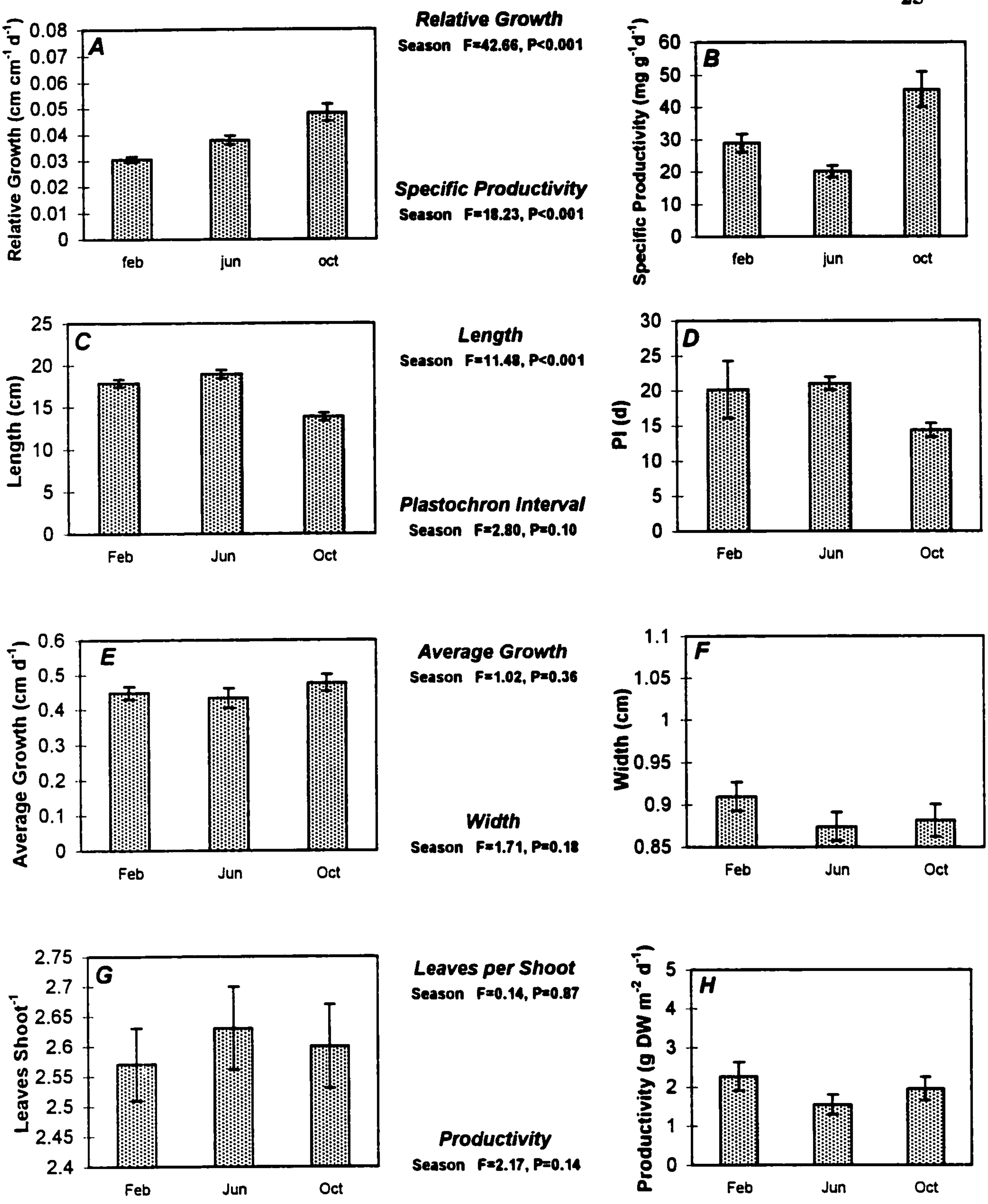
Figures 1.4A-H. Seasonal variation in *Thalassia* leaf growth at St. Lawrence. *(A)* Plastochron Interval, *(B)* Relative Growth Rate, *(C)* Average Growth Rate, *(D)* Leaf Length, *(E)* Leaf Width, *(F)* Leaves per Shoot, *(G)* Productivity and *(H)* Specific Productivity Rate. Values represent means ± SE (N=80; except PI, Productivity and Specific Productivity Rate where N=8). ANOVA results presented. Variables as defined in Methods.

$P<0.01$). For leaf growth rate and relative leaf growth rate, values were highest in October (Figures 1.4B,C; relative leaf growth rate: October>February, q=0.24, $P<0.001$; leaf growth rate: October>June, q=0.17, $P<0.001$; June>February, q=0.08, $P<0.01$). There was no effect of year and no significant interaction effect between year and season for any of the growth variables at St. Lawrence except leaves per shoot (Figures 1.4A-G). For leaves per shoot, there was a significant effect of year, but no interaction effect (Figure 1.4F).

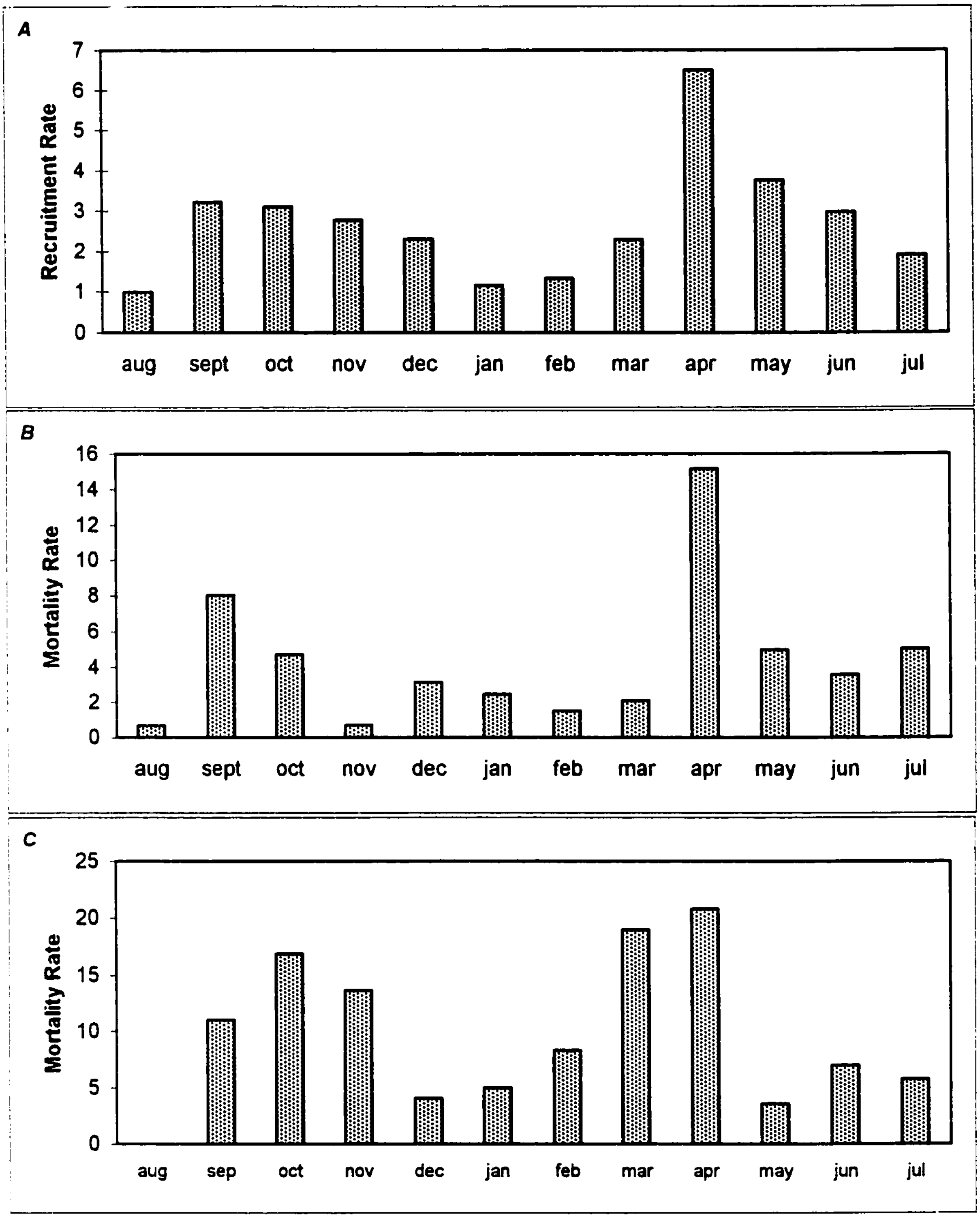
At Bath, there was a significant effect of season on relative leaf growth rate (Figure 1.5A), specific leaf productivity rate (Figure 1.5B) and leaf length (Figure 1.5C), a weak effect of season on plastochron interval (Figure 1.5D), but no effect of season on leaf growth rate (Figure 1.5E), leaf width (Figure 1.5F), leaves per shoot (Figure 1.5G) or leaf productivity (Figure 1.5H). As for St. Lawrence, values for relative leaf growth rate were highest and values for plastochron interval lowest in October, and specific leaf productivity rate was also highest in October (Figure 1.5A; Tukey's HSD test; for relative leaf growth rate: October>February, q=0.36, $P<0.001$; October>June, q=0.18, $P<0.001$; June>February, q=0.18, $P<0.001$; Figure 1.5B, for specific leaf productivity rate: October>February, q=0.041, $P<0.02$; October>June, q=0.07, $P<0.001$ for plastochron interval, Figure 1.5D). Leaf length values were lowest in October (Figure 1.5C; October<February, q=0.29, $P<0.001$, October<June, q=0.34, $P<0.001$).

### 1.4.2 Seasonal Changes in Shoot Recruitment and Shoot Mortality

Shoot recruitment at St. Lawrence (shown in Figure 1.6A as % recruitment to the 10 quadrats in each month) occurred at low levels throughout the year. A Friedman's two-way analysis of variance did not detect significant differences between months ($\chi_r^2=13.35$, $P=0.30$). However, a graphical display of the data suggests the possibility of seasonal bimodality in recruitment rates with peaks in September to November, and March to April (Figure 1.6A).



Figures 1.5A-H. Seasonal variation in *Thalassia* leaf growth at Bath. *(A)* Relative Growth Rate, *(B)* Specific Productivity, *(C)* Leaf Length, *(D)* Plastochron Interval, *(E)* Average Growth Rate, *(F)* Leaf Width, (G) Leaves per Shoot and *(H)* Productivity. Values represent means ± SE (N=100; except PI, Productivity and Specific Productivity Rate where N=10). ANOVA results presented. Variables as defined in Methods.



**Figures 1.6A-C. Seasonal variation in *Thalassia* shoot recruitment and shoot mortality at St. Lawrence. *(A)* Shoot Recruitment Rate in each month (number of recruits as % of the shoots present in the 10 quadrats in a month), *(B)* Mortality Rate of Mature Shoots in each month (number of shoots dying as % of the shoots in the 10 quadrats in a month), and (C) Mortality Rate of Young (<1 yr) Shoots (number of young shoots dying as % of the total young shoots monitored in a month).**

For mature shoots, monthly mortality rate (% of shoots dying) differed significantly between months (Friedman's two-way analysis of variance; $\chi_r^2$=24.32, P<0.01), with mortality peaks evident in September-October and in April (Figure 1.6B). Monthly mortality rate was positively correlated with monthly recruitment (Spearman Rank Correlation; $r_s$=0.65, P<0.05).

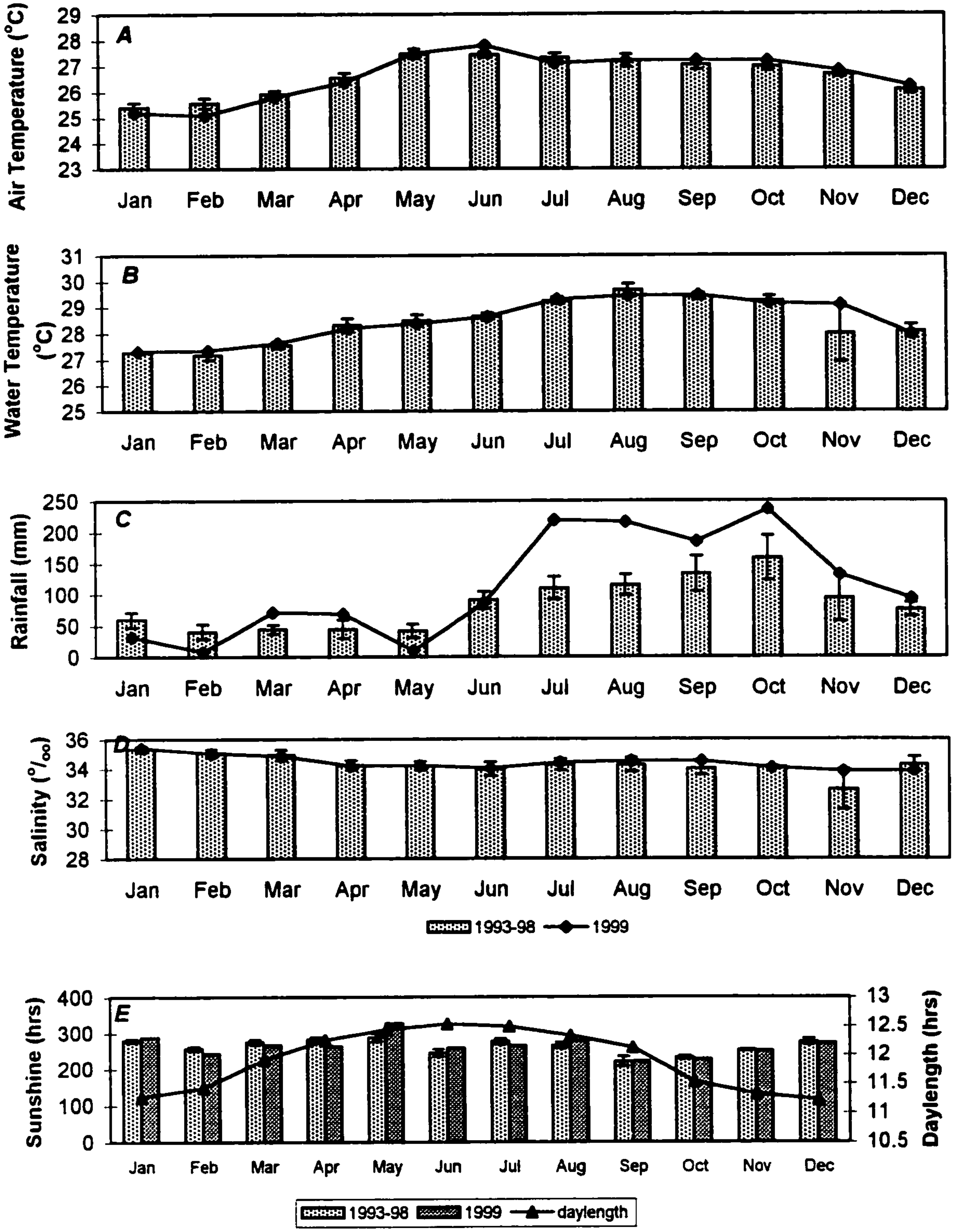
For shoots younger than 1 year, monthly mortality rate again tended to differ between months (Friedman's two-way analysis of variance; $\chi_r^2$=17.15, P=0.11), with mortality peaks evident in September to November, and in March to April (Figure 1.6C). Monthly mortality rate was again positively correlated with monthly recruitment (Spearman Rank Correlation; $r_s$=0.73, P<0.001).

## 1.4.3 Seasonal Variation in Environmental Variables

### 1.4.3.1 *Physical Variables*

For both the 6-year (1993-98) data set and the 1999 data set, monthly air temperature was highest between May and October (Figure 1.7A). Mean monthly air temperature values in the 1999 data set did not differ from those in the 1993-98 data set, indicating that 1999 was a typical year in terms of air temperature (Wilcoxon Paired-Sample Test; Z=0.16, P=0.88).

For the 6-year data set, monthly water temperature at St. Lawrence was highest between July and October; for 1999, the high values were retained through November (Figure 1.7B). The onset of highest water temperature values lags the onset of highest air temperature values by about 3 months (compare Figures 1.7A and 1.7B). Mean monthly water temperature values in 1999 did not differ from those in the 1993-98 data set, indicating that 1999 was a typical year in terms of water temperature (Wilcoxon Paired-Sample Test; Z=0.24, P=0.81).



Figures 1.7A-E. Seasonal variation in physical variables. Data on air temperature, rainfall daylength and sunshine were collected at the meteorological station nearest the St. Lawrence and Bath sites; values are monthly means of daily measurements ± SE. Data on water temperature and salinity were taken at the St.Lawrence site; values are means of weekly measurements ± SE.

For both the 6-year and the 1999 data sets, monthly rainfall was highest between June and November (Figure 1.7C). Mean monthly rainfall in 1999 did not differ significantly from the 1993-98 rainfall data set, indicating that 1999 was a typical year in terms of rainfall (Wilcoxon Paired-Sample Test; Z=1.26, P=0.21). However, there is some indication that rainfall in the wetter months in 1999 was higher than in 1993-98 (Figure 1.7C).

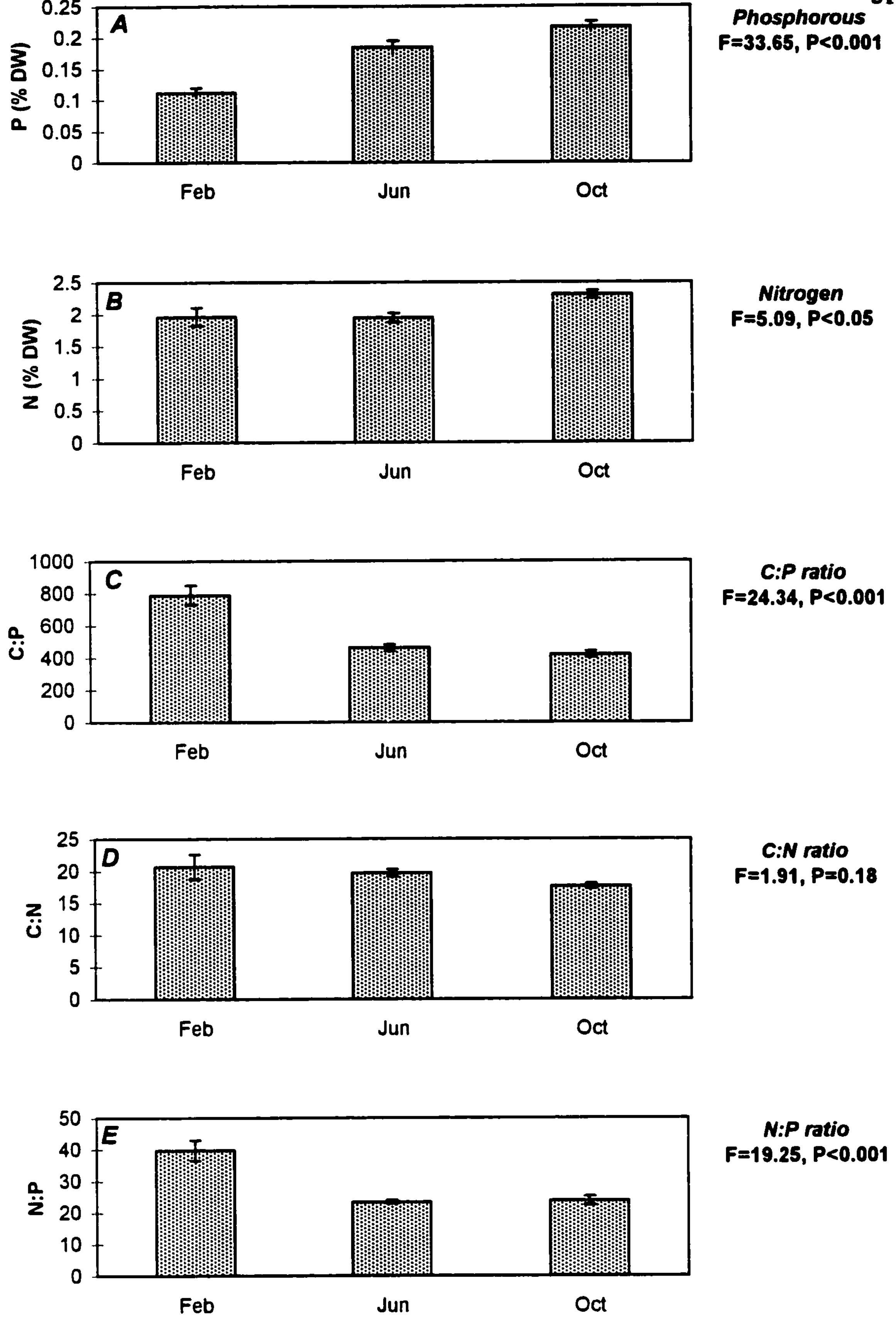
Seasonal variation in salinity at St. Lawrence was not strong, but values tended to be lower between April and November than between December and May (Figure 1.7D). Mean monthly salinity in 1999 did not differ significantly from the 1993-98 salinity data set, indicating that 1999 was a typical year in terms of salinity at the site (Wilcoxon Paired-Sample Test; Z=1.16, P=0.25). However, salinity in November 1999 was substantially higher than typical for November (Figure 1.7D). The seasonal decline in salinity values (April; Figure 1.7D) precedes the seasonal increase in rainfall (June; Figure 1.7C), and the higher rainfall in 1999 than 1993-98 did not result in lower salinity in 1999 (compare Figures 1.7C and 1.7D). These observations suggest that factors other than local rainfall influence variation in salinity of coastal waters at Barbados. The early seasonal decline in salinity suggests that a major factor may be effects of Amazon river discharge, which are detectable in Barbados' coastal waters between April and September, when the Guyana current brings oceanic water of reduced salinity towards Barbados from the South American mainland.

Total monthly sunshine values showed no clear seasonal trend, but may be lowest between September and November (Figure 1.7E). Monthly hours of sunshine in 1999 did not differ from the 1993-98 data set (Figure 1.7E; Wilcoxon Paired-Sample Test; Z=0.24, P=0.81). Seasonal variation in hours of sunshine was not correlated with seasonal variation in daylength (Figure 1.7E; Spearman Rank Correlation; $r_s$=0.06, P=0.96), presumably because of greater cloud cover in the wetter months (June to November; Figure 1.7C), some of which have long daylength (June to August; Figure 1.7E). Hours of sunshine may be lowest between September and November through the combined effects of shortening daylength and greater cloud cover.

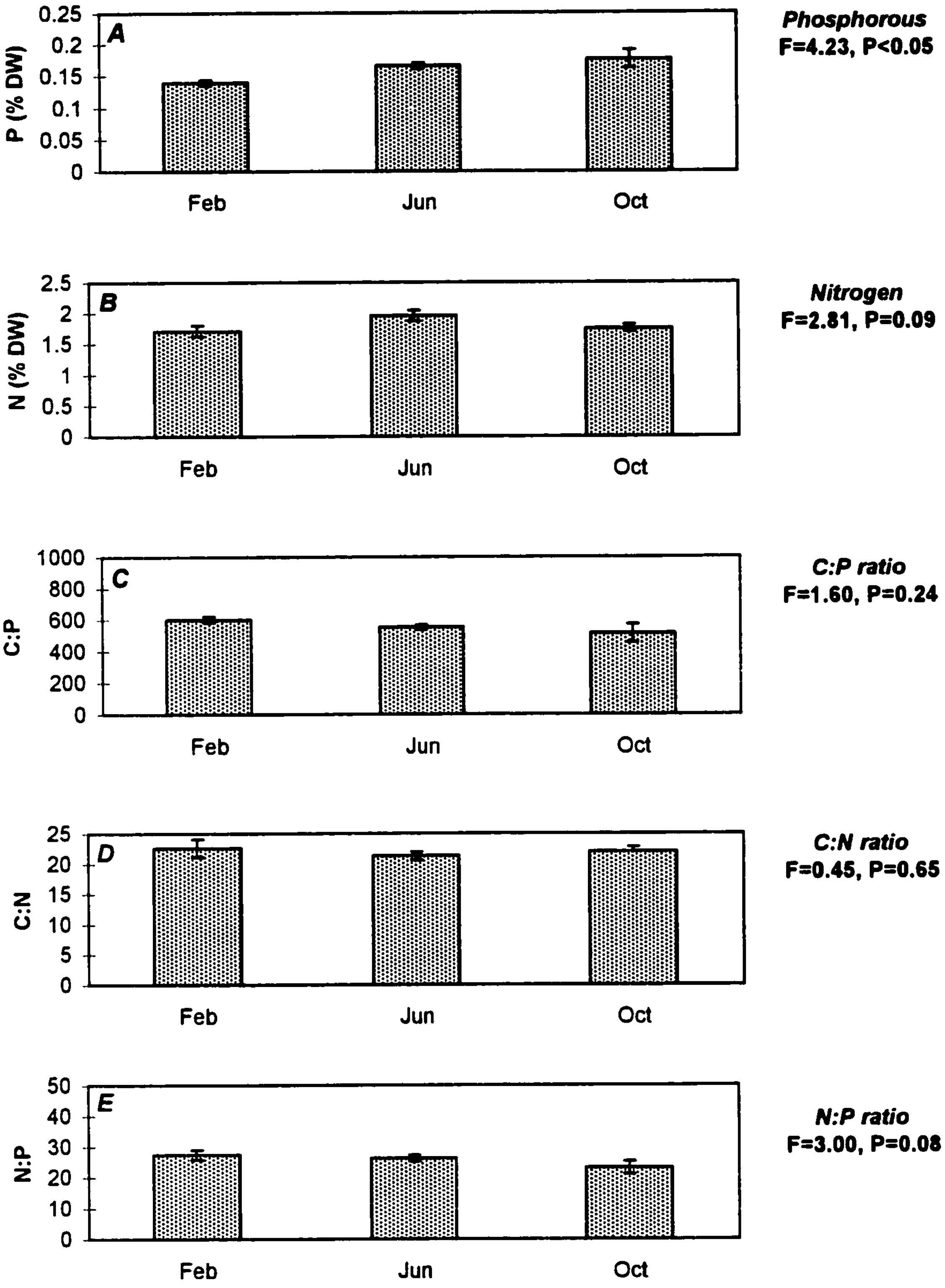
### 1.4.3.2 *Nutrient Concentrations*

At St. Lawrence, there was a significant effect of season on both total phosphorous (TP) content (Figure 1.8A) and total nitrogen (TN) content (Figure 1.8B) of *Thalassia* leaves. For both P and N, values were highest in October (Figure 1.8A,TP, Tukey's HSD test: October>February, q=1047.75, $P<0.001$; October>June, q=730.25, $P<0.05$; Figure 1.8B, TN, October>February, q=3445.0, $P<0.05$; October>June, q=3625.0, $P<0.05$). This suggests that both phosphorous and nitrogen may be more available to the *Thalassia* plants in October than in February and June. Consistent with this, there was a significant effect of season on C:P ratios (Figure 1.8C). Values were higher in February than in June and October (Figure 1.8C; Tukey's HSD test: February>June, q=328.99, $P<0.001$; February>October, q=371.70, $P<0.001$), indicating that phosphorous was less limiting in the latter months. C:N ratios also tended to be higher in February than June and October, but the difference between months was not statistically significant (Figure 1.8D). There was a significant effect of season on N:P ratios (Figure 1.8E), with values in February being higher than in June and October (February>June, q=16.28, $P<0.001$; February>October, q=15.83, $P<0.001$). The fact that N:P ratios are highest in the month when nutrients are most limiting (February), suggests that *Thalassia* plants at St. Lawrence may be more P-limited than N-limited.

At Bath, there was a significant effect of season on phosphorous content of *Thalassia* leaves (Figure 1.9A), and a weak effect of season on leaf nitrogen content (Figure 1.9B). For phosphorous, values were higher in October and June than in February, with the difference between October and February being statistically significant (Figure 1.9A; Tukey's HSD test: q=366.25, $P<0.05$). This suggests that phosphorous may be more available to the *Thalassia* plants in June and October than in February. For nitrogen, values were highest in June (Figure 1.9B), perhaps indicating greatest availability to the *Thalassia* plants in that month. Neither C:P nor C:N ratios differed significantly between months (Figures 1.9C and D), but the seasonal trends mirrored seasonal variation in P and N concentrations. C:P ratios tended to be highest in February (Figure 1.9C) when phosphorous concentrations were lowest



**Figures 1.8A-E. Seasonal variation in leaf tissue nutrient concentrations at St. Lawrence. Values represent means ± SE (N=8). ANOVA results presented.**



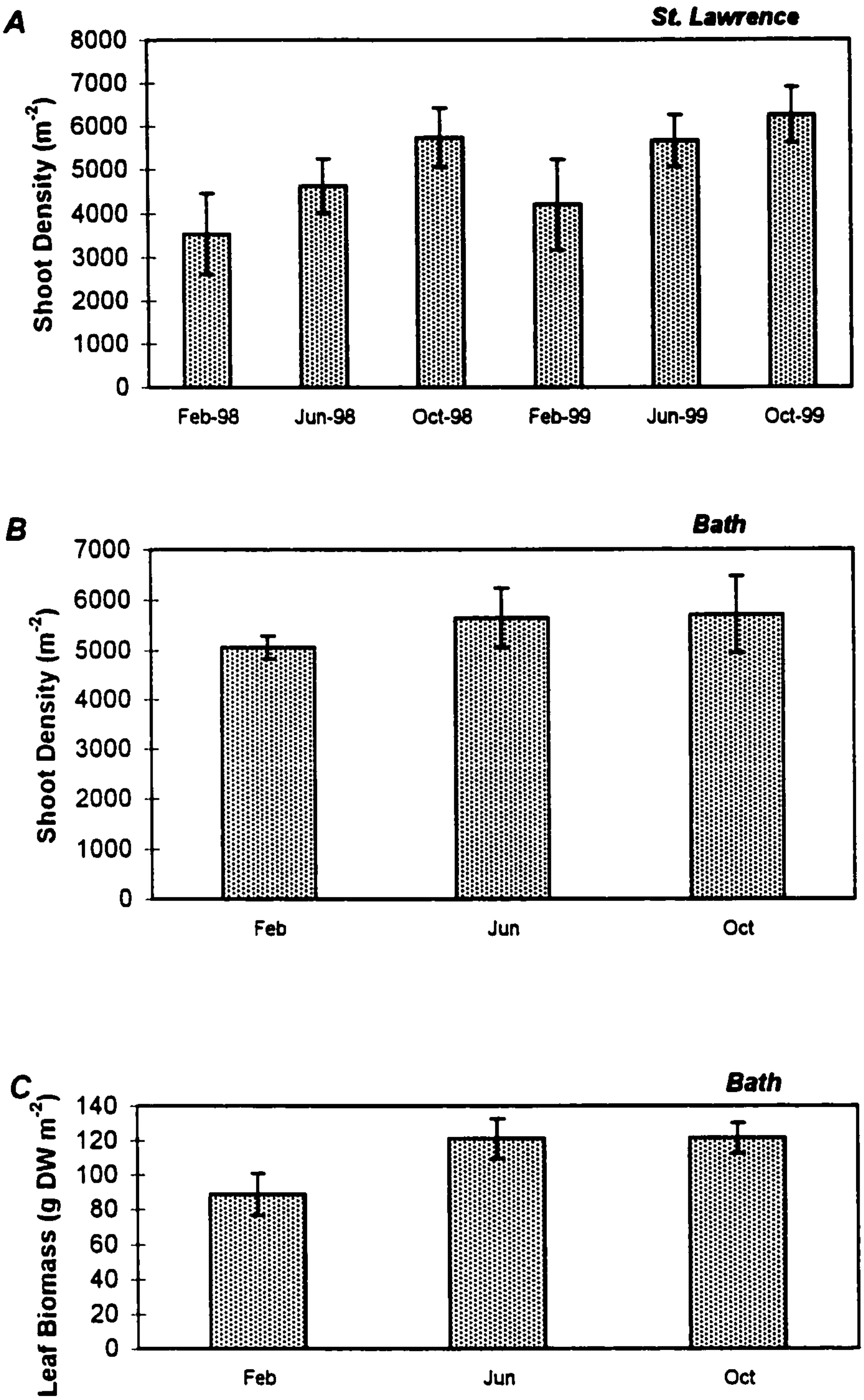
**Figures 1.9A-E. Seasonal variation in leaf tissue nutrient concentrations at Bath. Values represent means ± SE (N=10). ANOVA results presented.**

(Figure 1.9A), and C:N ratios tended to be lowest in June (Figure 1.9D) when nitrogen concentrations were highest (Figure 1.9B). There was a weak seasonal effect on N:P ratios (Figure 1.9E), with phosphorous being more limiting relative to nitrogen in February and less limiting relative to nitrogen in October (Figure 1.9E).

### 1.4.3.3 *Syringodium Abundance*

At St. Lawrence, there was a significant effect of season and a weak effect of year on *Syringodium* shoot density, but no interaction between season and year (Figure 1.10A). Shoot density was lower in February than in June and October, and lower in June than in October (Tukey's HSD test: February<June, $q=997.83$, $P<0.05$; February<October, $q=2134.83$, $P<0.001$; June<October, $q=1137.0$, $P<0.05$). Shoot density tended to be higher in 1999 than in 1998 (Figure 1.10A).

At Bath, there was no effect of season on *Syringodium* abundance as measured by shoot density (Figure 1.10B). However, there was a weak seasonal effect on *Syringodium* leaf biomass, with values in June and October tending to be higher than in February (Figure 1.10C).



**Season** F=14.87, P<0.001
**Year** F=3.01, P=0.10

**Season** F=0.47, P=0.63

**Season** F=2.85, P=0.09

Figures 1.10A-C. Seasonal variation in *Syringodium* abundance at *(A)* St. Lawrence, as measured by shoot density, at *(B)* Bath, as measured by shoot density, and at (C*)* Bath, as measured by leaf biomass. Values represent means ± SE (N=6 for St. Lawrence; N=9 for Bath). ANOVA results presented.

## 1.5 DISCUSSION

Consistent with the low latitude location of Barbados (Figure 1.1), there was only modest seasonal variation in air temperature, water temperature and daylength at the Barbados study site (Figure 1.7). By contrast, there was strong seasonal variation in rainfall, with most rain occurring between June and November (Figure 1.7). Rainfall could influence seagrass growth and abundance through associated cloud cover, effects on salinity and turbidity, and flushing of land-based nutrients into the coastal zone. Seasonal variation in salinity and in hours of sunshine at the Barbados study sites was small, although hours of sunshine were somewhat lower in the later rainy months, September to November (Figure 1.7). Seasonal variation in turbidity was not measured in this study. Qualitative observations suggest that episodic turbidity increases do occur during bouts of extreme rainfall, particularly in more agricultural areas, such as the Bath site. However, the exposed nature of the Bath site results in quick dispersion of the turbid water mass. In terms of nutrient discharge, Lewis (1987) and Wellington (1999) have shown that nutrient concentrations in the Barbados coastal zone tended to be higher in the rainy season than in the dry season. McMahon and Walker (1998) documented a similar phenomenon in Geographe Bay, Australia, and further showed that nutrient concentrations in seagrasses in the Bay increased in response to the increased nutrient input.

Seasonal variation in nutrient coastal levels should reflect both seasonal variation in the strength of the land-based source and seasonal variation in input rates through rainfall and coastal discharge. At St. Lawrence, the principal land-based nutrient source is domestic sewage, which enters the coastal zone primarily as sub-surface ground water discharge. Sewage is generated at a similar rate throughout the year since coastal population density changes little throughout the year, and its presence in the coastal zone should therefore reflect discharge rates to the coastal zone driven by, but slightly lagged on, rainfall. Consistent with this, there was significant seasonal variation in total nitrogen and phosphorous contents of *Thalassia* leaves at St. Lawrence, with phosphorous and nitrogen values in October being higher (and C:P and C:N ratios lower) than in June and February (Figures 1.8A,B; compare with Figure 1.7C). At Bath, the principal land-based nutrient source is agricultural fertiliser, although sewage discharge also occurs. Discharge enters the coastal zone as both surface and sub-surface run-off. Annual fertiliser application rates are highest in early summer (June; D. Marshall, Buttals Plantation *pers. comm.*) and this, coupled with rainfall-driven surface and sub-surface discharge rates, should primarily drive seasonal variation in coastal nutrient values at Bath. Consistent with this suggestion, seasonal variation in phosphorous content of *Thalassia* leaves, and to a lesser extent nitrogen content of the leaves, was detectable at Bath, with phosphorous values being higher (and C:P values lower) in October and June than in February, and nitrogen values being highest (and C:N values lowest) in June (Figures 1.9A,B; compare with Figure 1.7C). Since *Thalassia* in Barbados is believed to be nutrient-limited (Patriquin 1972), seasonal variation in nutrient availability, and hence in degree of nutrient limitation, might be expected to result in seasonal variation in *Thalassia* growth variables. The suggestion that *Thalassia* in Barbados is nutrient-limited is supported by the present results which indicate that, particularly in February when nutrients are most limiting, leaf tissue nutrient levels are below or near those suggested by Duarte (1990) as indicating levels at which seagrasses are likely to be nutrient-limited (1.82 % N, 0.20 % P; in this study in February at St. Lawrence, values were 1.96 % N and 0.11 % P; in February at Bath, 1.71 % N and 0.14 % P).

Four of the *Thalassia* growth variables in this study are rate variables and are not area-specific. These are plastochron interval, leaf growth rate, relative leaf growth rate and specific leaf productivity rate. There was significant seasonal variation in plastochron interval at St. Lawrence, and a weak effect of season on plastochron interval at Bath. At both sites, plastochron interval was lowest in October, i.e. leaves were produced fastest at the time when nutrient availability, as indicated by leaf nutrient content, was greatest. At St. Lawrence, both phosphorous and nitrogen were most available in October; at Bath, phosphorous, but not nitrogen, was most available in October, and the present results suggest that phosphorous may be more limiting than nitrogen at both study sites. There was a weak effect of season on leaf growth rate at St. Lawrence, but no significant variation in leaf growth rate at Bath. At St. Lawrence, the leaf growth rates were again highest in October, when nutrient availability is assessed to be highest (note the same, but non-significant, trend at Bath; Figure 1.5). Consistent with the trends in plastochron interval and leaf growth rate, there was significant seasonal variation in relative leaf growth rate at both St. Lawrence and Bath, with rates (linear rate of production of new leaf material per unit of old leaf material present) being highest at both sites in October, when nutrient availability is highest. Specific leaf productivity rate (a measure of production rate of new leaf material in weight per unit of old leaf material present) did not differ significantly at St. Lawrence, but was also highest in October at Bath. The only other leaf variable which showed seasonal variation was leaf length, which varied significantly at Bath. Leaves at Bath were smallest in October. This is consistent with the high rate of leaf production at Bath in October and the lack of significant variation in leaf growth rates at that site, i.e. there are more young leaves, and hence a smaller average leaf length, at Bath in October. At St. Lawrence, leaves are not smallest in October despite the rate of leaf production being highest at that time, presumably because leaf growth rates are highest in that period.

It is important to note that data on *Thalassia* leaf growth variables are available for 2 years at St. Lawrence, and that for none of the growth variables for which significant variation was detected between times of year (February, June, October) was there a significant interaction effect between time of year and year. This indicates that, for all of these variables, the pattern of variation within a year was the same in both years, supporting the contention that the variation observed was indeed seasonal.

The present results therefore suggest that variation in *Thalassia* leaf growth rate variables within a year may indeed be seasonal, and may be driven by seasonal variation in nutrient availability. The suggestion that seagrasses at St. Lawrence and Bath may be influenced by seasonal variation in nutrient availability is supported by the results obtained on seasonal variation in abundance of *Syringodium filiforme*. There was a significant seasonal effect on

*Syringodium* abundance at St. Lawrence, and a weak seasonal effect on *Syringodium* abundance at Bath, with abundance being highest in the months in which nutrient availability is suggested to be highest. Specifically, at St. Lawrence, *Syringodium* abundance was highest in October when nitrogen and phosphorous availability is highest and least limiting (Figure 1.10A; compare with Figures 1.8A-D). At Bath, *Syringodium* abundance tended to be higher in October and June than in February, and nutrient availability is suggested to be lowest and most limiting in February (Figures 1.10B,C; compare with Figures 1.9A-D). *Syringodium* is considered to be an earlier successional stage than *Thalassia* in the seral development of Caribbean seagrass communities (den Hartog 1971; Patriquin 1975; Zieman 1976), and may therefore be expected to respond rapidly to increased nutrient inputs in nutrient-limited environments (Williams 1987, 1990). As was the case for the *Thalassia* leaf growth variables, variation in *Syringodium* abundance at St. Lawrence within a year did not differ between years (i.e. no significant interaction effect between time of year and year), supporting the suggestion that the variation in *Syringodium* abundance observed within a year is a seasonal pattern.

In contrast to *Thalassia* growth rate variables, *Thalassia* demographic variables do not appear to be driven by seasonal variation in nutrient availability. Seasonal variation in shoot recruitment appeared to be bimodal, with peaks in fall (September-November) and spring (March-April). The former period coincides with the period of high nutrient availability, the latter does not. Interestingly, both Zieman (1975b) and Durako (1994) report bimodal seasonal variation in shoot recruitment of *Thalassia* in Florida, with peaks around spring and fall. The fact that seasonal variation in shoot recruitment of *Thalassia* appears similar across sub-tropical (Florida) and tropical (Barbados) areas may suggest that it reflects an endogenous rhythm characteristic of the plant, rather than being a response to seasonally-driven environmental variation.

Mortality of both young and mature *Thalassia* shoots at St. Lawrence differed between months, with the difference being statistically stronger for mature shoots. For both age categories, mortality peaks were evident around September-November and April-May. Monthly mortality of both age categories was positively correlated with monthly recruitment. This suggests that the *Thalassia* population at St. Lawrence may be close to a shoot density carrying capacity, and that the increased mortality associated with recruitment pulses is spread across age classes, i.e. is not restricted to the new recruits. The correlation of mortality with recruitment implies that marked seasonal variation in shoot density need not occur despite the seasonal variation in recruitment. I was unable to discover prior studies of seasonal variation in *Thalassia* shoot mortality. However, Durako (1994) remarked that recruitment balanced mortality at 2 of his 3 *Thalassia* study sites in Florida Bay, an observation which is consistent with the present results. Interestingly, Vermaat *et al.* (1995) reported that annual mortality rates were closely correlated with annual recruitment rates for *Enhalus acoroides*, *Cymodocea serrulata*, *Halodule uninvervis* and *Syringodium isoetifolium* in the Philippines, and Duarte *et al.* (1996) reported a similar result for *Thalassodendron ciliatum* in Kenya.

Consistent with the observation that monthly mortality was correlated with monthly recruitment in the present study, there was no effect of season on *Thalassia* shoot density at Bath, and only a weak effect of season on shoot density at St. Lawrence, with shoot density tending to be lowest in October and highest in June. In contrast to shoot density, there was significant seasonal variation in leaf biomass at both St. Lawrence and Bath, with values being highest in June for St. Lawrence and lowest in October for Bath (see Figures 1.2 and 1.3). The variation observed in leaf biomass and shoot density of *Thalassia* at St. Lawrence at different times of year did not differ between years (i.e. no significant interaction between time of year and year), supporting the suggestion that the variation observed is seasonal.

An important result of the present study is that seasonal variation in *Thalassia* demographic variables (shoot recruitment and shoot mortality) does not appear to be a response to seasonally-driven environmental variation, but that variation in leaf growth rate variables may be driven by seasonal variation in nutrient availability. Leaf growth rate variables appear to be highest when leaf tissue nutrient levels, which are used as an index of nutrient availability, are highest. The contention is that nutrient availability is a limiting factor whose seasonal variation drives seasonal variation in growth, i.e. the variation in growth is the consequence of the variation in nutrient availability. This differs from the situation with temperate seagrasses, where seasonal variation in growth is primarily driven by variation in temperature and light, and leaf nutrient levels are lowest when growth rates are highest, i.e. the variation in leaf nutrient levels is the consequence of the variation in growth (Perez-Llorens and Niell 1993).

In this study, in periods when nutrients are most limiting (as indicated by C:P and C:N ratios), phosphorous appeared to be more limiting than nitrogen (as indicated by high N:P ratios), and this was true for both the St. Lawrence and Bath study sites. Moreover, phosphorous levels in *Thalassia* leaves at both St. Lawrence (0.11 % in February) and Bath (0.14 % in February) were appreciably lower than the value suggested by Duarte (1990) as indicating phosphorous limitation (0.20 %), but nitrogen levels were either just below or above Duarte's suggested value for nitrogen (limiting value 1.82 %; St. Lawrence in February 1.96 %, Bath in February 1.71 %). The % P and %N values obtained in this study are in the same range as those reported by Fourqurean and Zieman (1992) for *Thalassia* in Florida Bay, where the *Thalassia* was concluded to be phosphorous-limited. These results indicate that *Thalassia* in Barbados may be phosphorous-limited, but this differs from the conclusion of Patriquin (1972) who suggested that *Thalassia* was more nitrogen-limited than phosphorous-limited in Barbados. It should be noted in this context that nitrogen loading of the Barbados coastal zone is estimated to have increased some 3- to 10-fold over the period 1977 to 1994 (Delcan 1995a; Halcrow 1998a; Chapter 5, this thesis). It is therefore possible that nitrogen loading may have switched *Thalassia* systems in Barbados from primarily nitrogen limitation in 1969 (Patriquin 1972) to primarily phosphorous limitation in 1999 (this study). Murray *et al.* (1992) have suggested that nutrient loading of the coastal zone in Chesapeake Bay, occuring through input of nitrogen contaminated ground water, switched *Zostera marina* stands in the Bay from primarily nitrogen limitation to primarily phosphorous limitation over a 12-year period.

# CHAPTER 2 EFFECTS OF SHOOT AGE ON LEAF GROWTH IN THE SEAGRASS *THALASSIA TESTUDINUM* IN BARBADOS

## 2.1 ABSTRACT

Effects of shoot age on leaf growth variables of *Thalassia testudinum* were investigated in St. Lawrence Bay, Barbados. The effects were investigated separately within 3 shoot age categories, those less than 1 year old (young shoots), those between 1.8 and 2.2 years old (old shoots), and those between 4.5 and 6.1 years old (oldest shoots). Shoot age affected all leaf growth variables investigated. Leaf width increased with shoot age in all 3 age categories, with age explaining 46% of the variance in leaf width in young shoots. Leaf growth rate increased with shoot age in young shoots, and weak positive effects were detectable in both older shoot categories. Plastochron interval and maximum leaf length increased with age for young shoots. The effects were detectable in old shoots, but not in the oldest shoot age category. Leaves per shoot increased with shoot age in both older age categories, but the amount of variance explained was low, and shoot age did not affect leaves per shoot in young shoots. Relative leaf growth rate was negatively correlated with age in young shoots, not correlated with age in old shoots, and positively correlated with age in the oldest shoots. The possibility of trend reversals between leaf growth variables and shoot age emphasises the need to assess effects of age within discrete age categories. For all leaf growth variables except leaves per shoot, the amount of variance in growth explained by shoot age was higher in young shoots than in older age categories. The only prior study of shoot age on leaf growth variables was on a temperate seagrass, *Cymodocea nodosa*, where positive effects of shoot age on leaf length and leaves per shoot were detected. The results of the prior and present study suggest that shoot age effects on leaf growth variables may be common in seagrasses, and that shoot age may have been largely overlooked as a component of the considerable spatial and temporal variation in leaf growth typically observed in seagrasses.

## 2.2 INTRODUCTION

Studies of environmental effects on seagrass growth are numerous, but only one study (Duarte and Sand-Jensen 1990) has provided data on effects of age on seagrass. Duarte and Sand-Jensen (1990) showed that leaves per shoot and leaf length (longest leaf on a shoot) increased with shoot age in the seagrass *Cymodocea nodosa* in the Mediterranean, with shoot age being measured in number of plastochron intervals (where a plastochron refers to the time interval between the formation of successive leaves on a shoot; Erickson and Michelini 1957; Jacobs 1979). Other studies have commented that leaf growth may be influenced by shoot age. For example, Zieman (1968) and Patriquin (1973) remarked that plastochron intervals may be shorter in very young shoots of *Thalassia testudinum*, and Kaldy *et al.* (1999) accepted this observation and adjusted for it in generating *Thalassia* age-frequency distributions. Durako (1995) observed temporal reductions in average leaf length and shoot specific leaf area in *Thalassia* in Florida Bay. He suggested that the reductions could either be responses to environmental stress or could reflect a shift in population demographics to younger shoots, assuming that shoot age affects leaves per shoot and leaf length in *Thalassia* as had been documented for *Cymodocea* (see Duarte and Sand-Jensen 1990).

Understanding whether shoot age affects seagrass growth variables is important in understanding spatial and temporal variation in growth. Seagrass beds are often characterised by considerable spatial variation, which is typically attributed to local environmental variation, but could have an age component. For example, shoots near the center of seagrass patches may be older than shoots near the periphery, which could influence differences in growth rates observed (Duarte and Sand-Jensen 1990). Seasonal variation in leaf growth is frequently observed, and is typically explained by seasonal variation in environmental conditions (e.g. water temperature and light: Barber and Behrens 1985; Alcoverro *et al.* 1995; Marba *et al.* 1996; see Chapter 1), but could partly result from effects of shoot age if shoot recruitment is seasonal and is strong enough to significantly affect population age structure. Finally, long term trends of a reduction in leaf growth may indicate reduced viability in response to chronic environmental stress, but could also reflect a shift to a younger age distribution resulting from recolonisation following significant disturbance events (see Durako 1994, 1995).

The objective of this Chapter is to investigate effects of shoot age on plastochron interval, average leaf growth rate, relative leaf growth rate, leaf length, leaf width and leaves per shoot in the seagrass *Thalassia testudinum* in Barbados.

## 2.3 METHODS

### 2.3.1 Study Location and Shoot Tagging

The study was conducted at St. Lawrence, on the south coast of Barbados (see Chapter 1, Section 1.3 for location and description of site). Effects of shoot age on *Thalassia testudinum* growth variables were examined separately for mature shoots (>1yr) and for young shoots (<1yr). In both cases, *Thalassia* shoots were individually tagged and monitored. Shoot tags consisted of a 4" nail with a small wire loop (3 cm diameter) wrapped around the nail head, and a small piece of brightly colored flagging tape affixed to the loop with an identification number unique to each shoot. A shoot was tagged by pulling all of its leaves through the wire loop, and inserting the full length of the nail into the substrate such that only the numbered flagging tape protruded from the substrate. The tags were not in physical contact with the shoot, and therefore should not have impeded leaf movement or growth.

### 2.3.2 Mature Shoots

Four hundred shoots were individually tagged in ten 25 cm x 25 cm (0.0625 $m^2$) quadrats, each randomly placed and permanently fixed in each of the 10 largest seagrass stands in St. Lawrence Bay. The shoots were monitored for a 6 month period (February to July 1998). Plastochron interval (days) was measured continuously for all tagged shoots at all sites throughout the 6 month period by monitoring new leaf production every other day, and calculating the time between emergence of 2 successive leaves. The values obtained were averaged for each shoot. Average leaf growth rate per shoot (cm $d^{-1}$), relative leaf growth rate per shoot (cm new tissue • $cm^{-1}$ old tissue • $d^{-1}$), maximum leaf length (longest leaf on a shoot; cm), leaf width (cm) and leaves per shoot were measured for all shoots in the final month of the study (July 1998). Measurement details for the growth variables (except PI) are as provided in Section 1.3.2.2. At the end of the study (August 1998), shoots were excavated with rhizomes intact (i.e. shoots remained attached to the horizontal rhizome), and aged in plastochron interval (PI) units by counting the number of leaf scars on each shoot (vertical rhizome). Two hundred and one of the original 400 shoots were successfully excavated (i.e. vertical rhizomes and leaves intact) and could therefore be aged. Mean shoot age in PI units in the 10 quadrats ranged from 34 to 104, and differed significantly between quadrats (one-way ANOVA; F=10.83, P<0.001). Quadrats were therefore not pooled to assess effects of age on growth, since apparent effects of age could have been generated by environmental differences between the sites where the quadrats were located. However, 4 of the 10 quadrats had a "younger" shoot age distribution (range of means: 34-41 PI units), and the remaining 6 quadrats had an "older" shoot age distribution (range of means: 77-104 PI units). Effects of shoot age on the growth of mature shoots were therefore determined using linear regression analyses conducted separately for 2 categories of quadrats, those with younger shoot age distributions (subsequently termed "old shoots"), and those with older shoot age distributions (subsequently termed "oldest shoots"). Shoot age distributions did not differ between the 4 quadrats with old shoots, nor between the 6 quadrats with older shoots (quadrats with old shoots: F=0.77, N=75, P=0.47; quadrats with oldest shoots: F=1.59, N=126, P=0.18). Consequently, any correlations detected between shoot age and leaf growth variables within each of the two age categories can not spuriously arise from environmental effects on the growth variables and differences in shoot age at the different sites (quadrats).

### 2.3.3 Young Shoots

Two hundred shoots were randomly selected on the day of their emergence from 10 quadrats near to (i.e. within a 2 m radius) the 10 sites used for monitoring the mature shoots, and were individually tagged and monitored over a 1-year period (August 1997 to August 1998). As for the mature shoots, the emergence of leaves to calculate plastochron interval was monitored every 2 days over a 6 month period (August 1997 to January 1998). Leaf growth rate, leaf length, leaf width and leaves per shoot were measured every second day over the same 6 month period. These growth variables, as well as relative leaf growth rate, were also measured at the end of 1 year (August 1998). Measurement details for the growth variables (except PI) are provided in 1.3.2.2. At the end of the study (in August 1998), 121 of the original 200 shoots were successfully excavated with rhizomes intact and aged; but chronological age, rather than age in PI units,was used to assess age effects on growth. The effects of shoot age on the growth variables were investigated by linear regression analysis in two ways; first, using only the growth data obtained on the single sampling occasion at the end of the 1 year period, and second, using the data measured every second day over the 6-month period. For the single sampling data set, PI was measured for each shoot by dividing the known chronological age of the shoot by the number of leaf scars on the shoot. For the continuous data set, PI was calculated from the continuous monitoring of leaf emergence on each shoot over the 6-month period, and the PI values obtained were averaged for each shoot.

## 2.4 RESULTS

### 2.4.1 Young Shoots

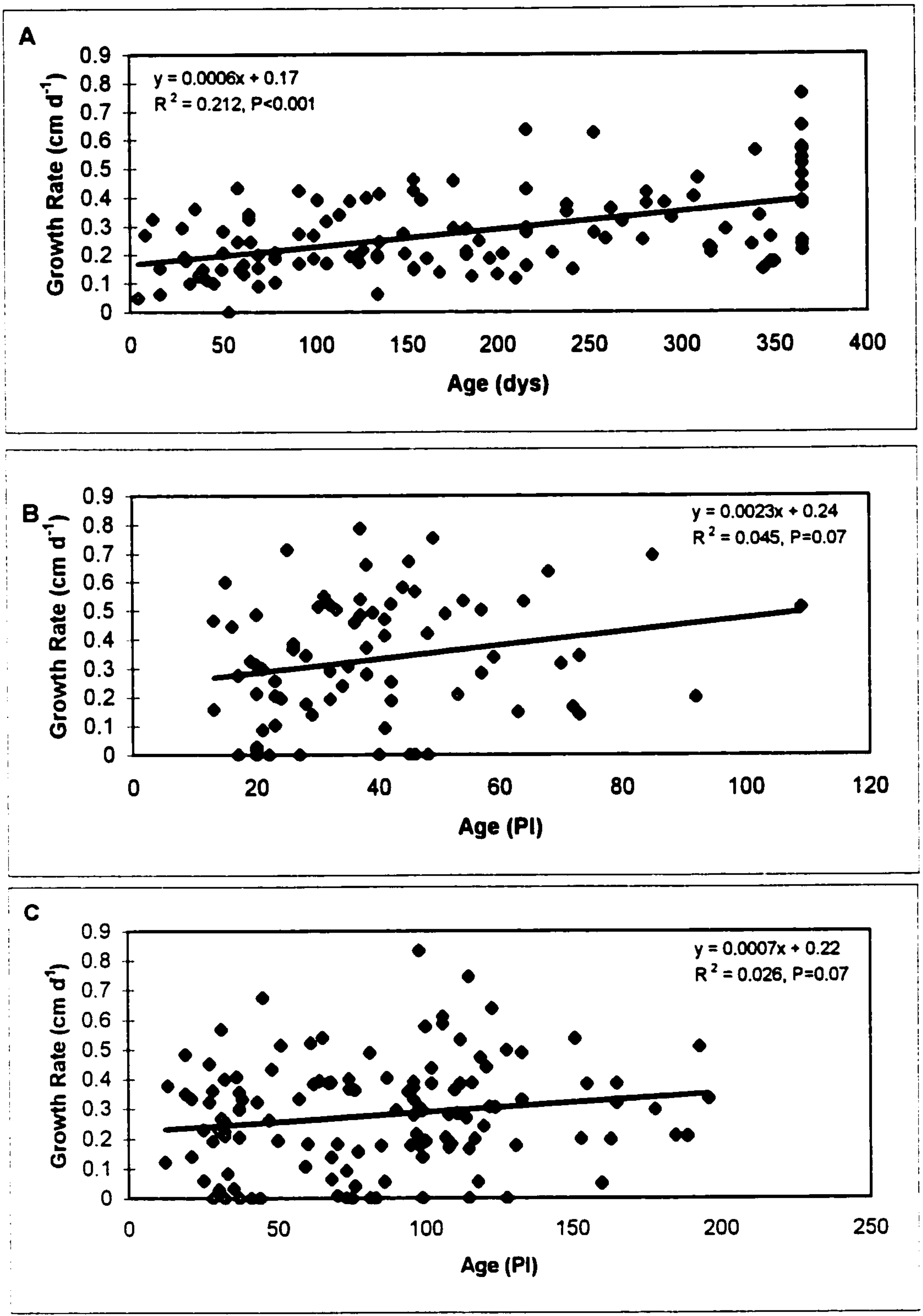
Shoot age significantly affected leaf growth variables in shoots less than one year old, as indicated by both the single sampling data set and the continuous sampling data set (see Section 2.3). For the former data set, leaf growth rate (Figure 2.1A; Linear Regression Analysis: $F=37.08$, $P<0.001$), maximum leaf length (Figure 2.2A; $F=144.30$, $P<0.001$), leaf width (Figure 2.3A; $F=101.97$, $P<0.001$) and leaf PI (Figure 2.4A; $F=75.14$, $P<0.001$) increased significantly with increasing shoot age, and relative leaf growth rate decreased significantly with shoot age (Figure 2.5A; $F=38.11$, $P<0.001$). There was no effect of shoot age on leaves per shoot (Figure 2.6A; $F=1.43$, $P=0.23$).

Identical results were obtained using the continuous sampling data set. Leaf growth rate ($F=110.89$, $R^2=0.202$, $P<0.001$), maximum leaf length ($F=972.38$, $R^2=0.688$, $P<0.001$), leaf width ($F=496.24$, $R^2=0.529$, $P<0.001$) and leaf PI ($F=54.12$, $R^2=0.252$, $P<0.001$) increased with shoot age, and there was no effect of shoot age on leaves per shoot ($F=0.01$, $R^2<0.01$, $P=0.93$). Data on relative leaf growth rate were not available from the continuous sampling data set.

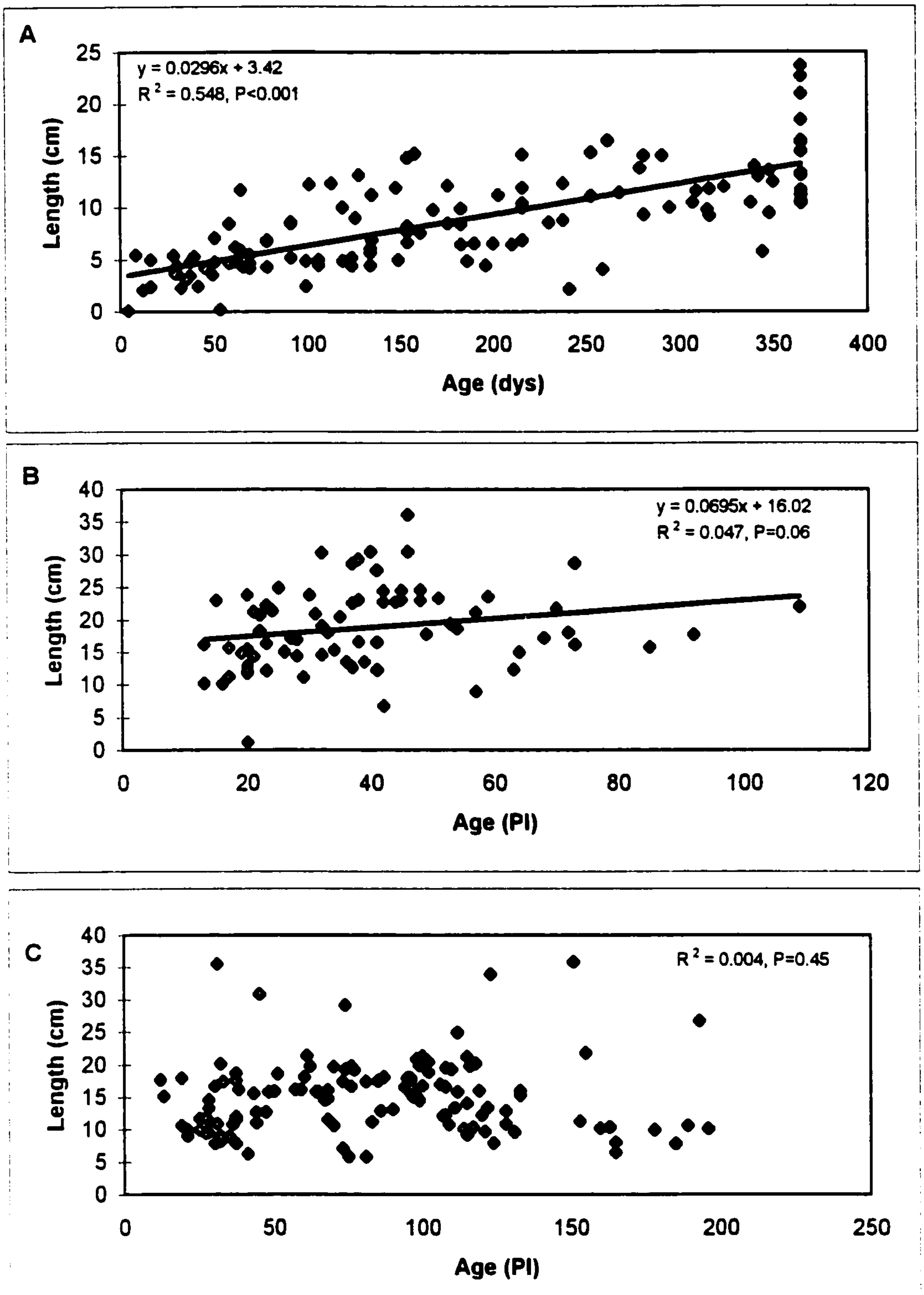
### 2.4.2 Mature Shoots

#### 2.4.2.1 *Old Shoots*

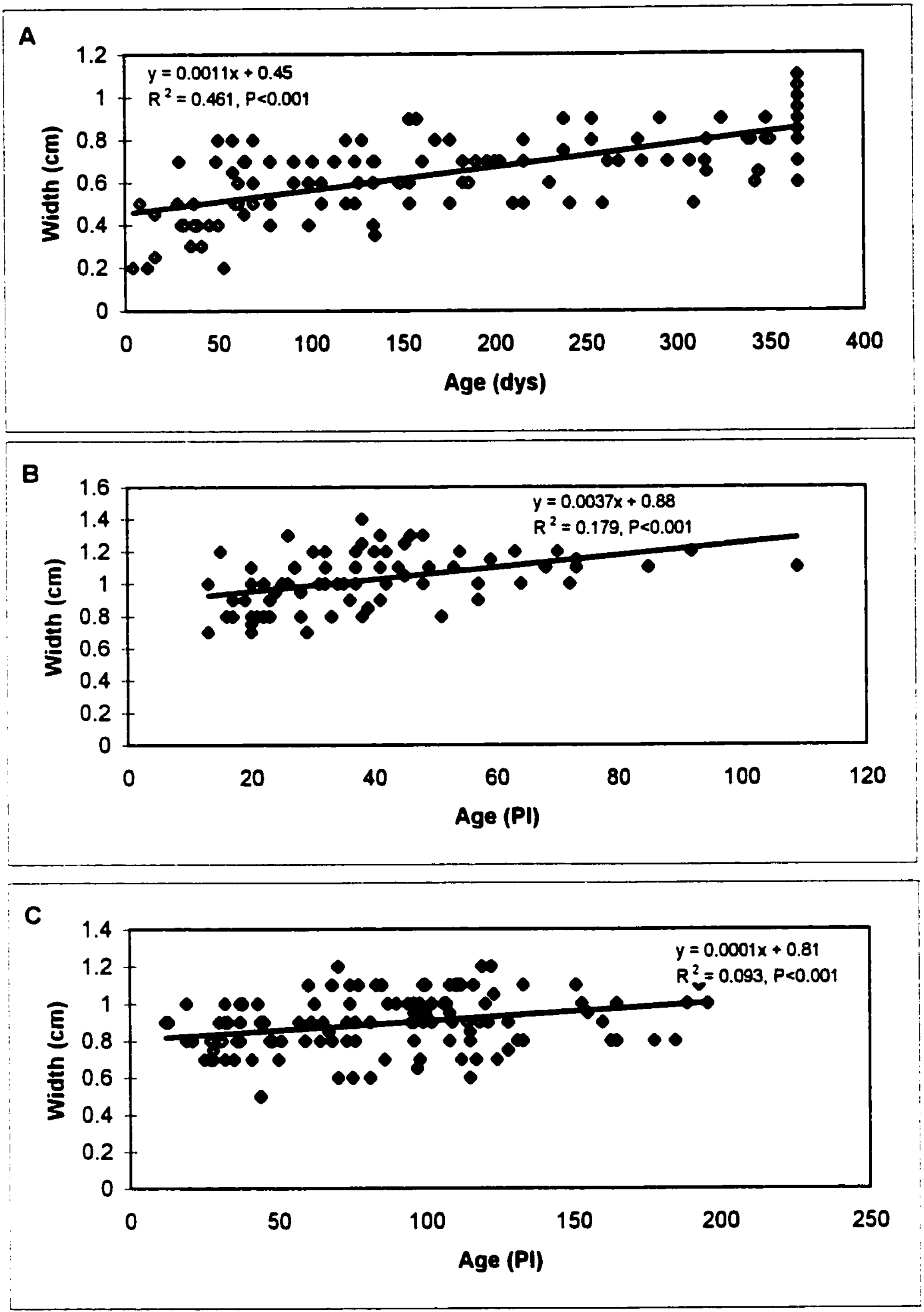
Shoot age also affected leaf growth in old shoots, i.e. shoots with mean ages between 34 and 41 PI units. There was a weak positive relationship between shoot age and leaf growth rate (Figure 2.1B; Linear Regression Analysis: $F=3.34$, $P=0.07$), between shoot age and maximum leaf length (Figure 2.2B; $F=3.60$, $P=0.06$), and between shoot age and leaf PI



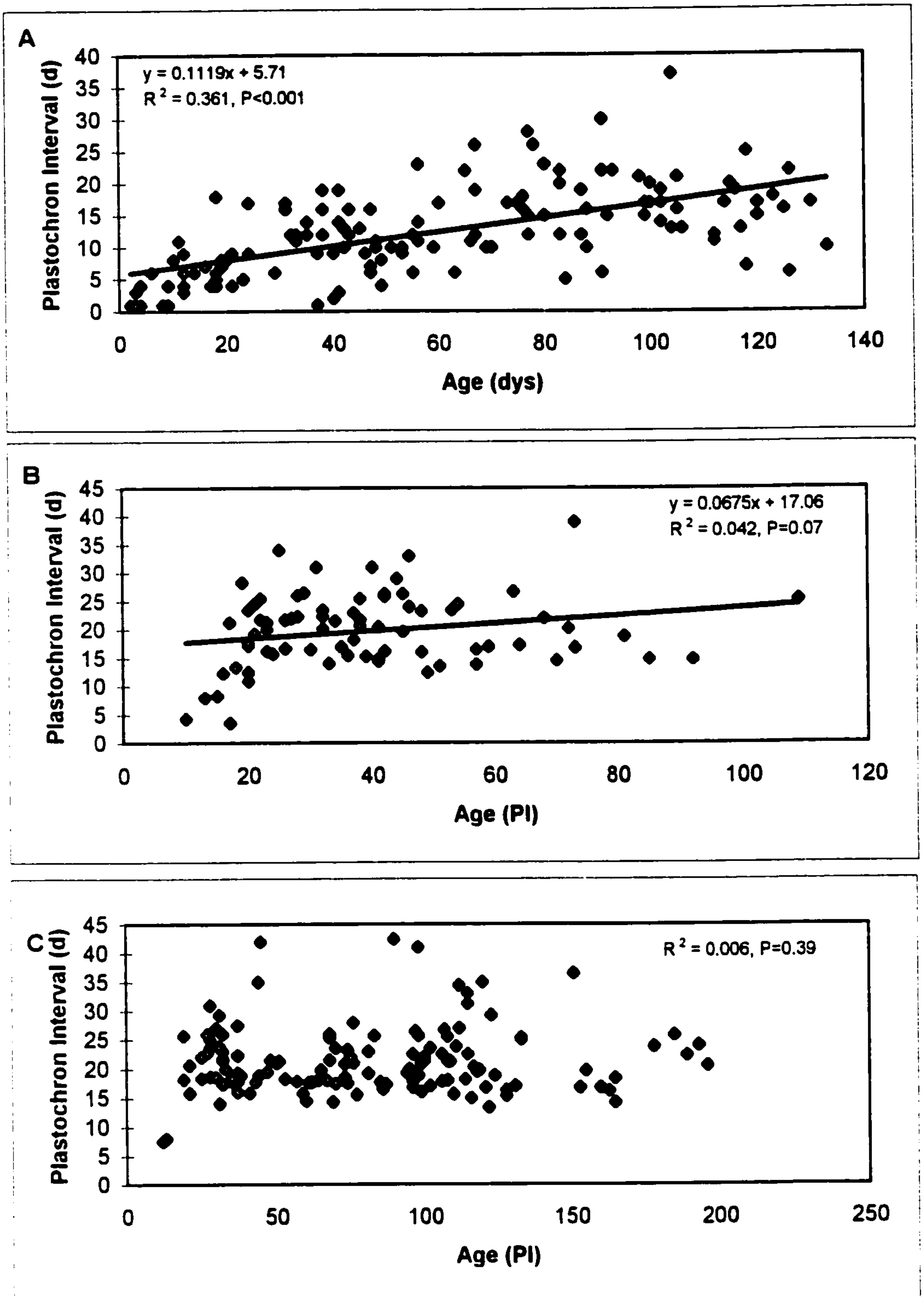
**Figures 2.1A-C. Linear regressions and regression equations of average leaf growth rate vs shoot age for young (< 1yr), old (mean PI = 39) and oldest (mean PI = 79) *Thalassia* shoots. Age is in chronological time for young shoots, and in PI units for old and oldest shoots. Data for young shoots are from the single sampling data set (see Section 2.3.3).**



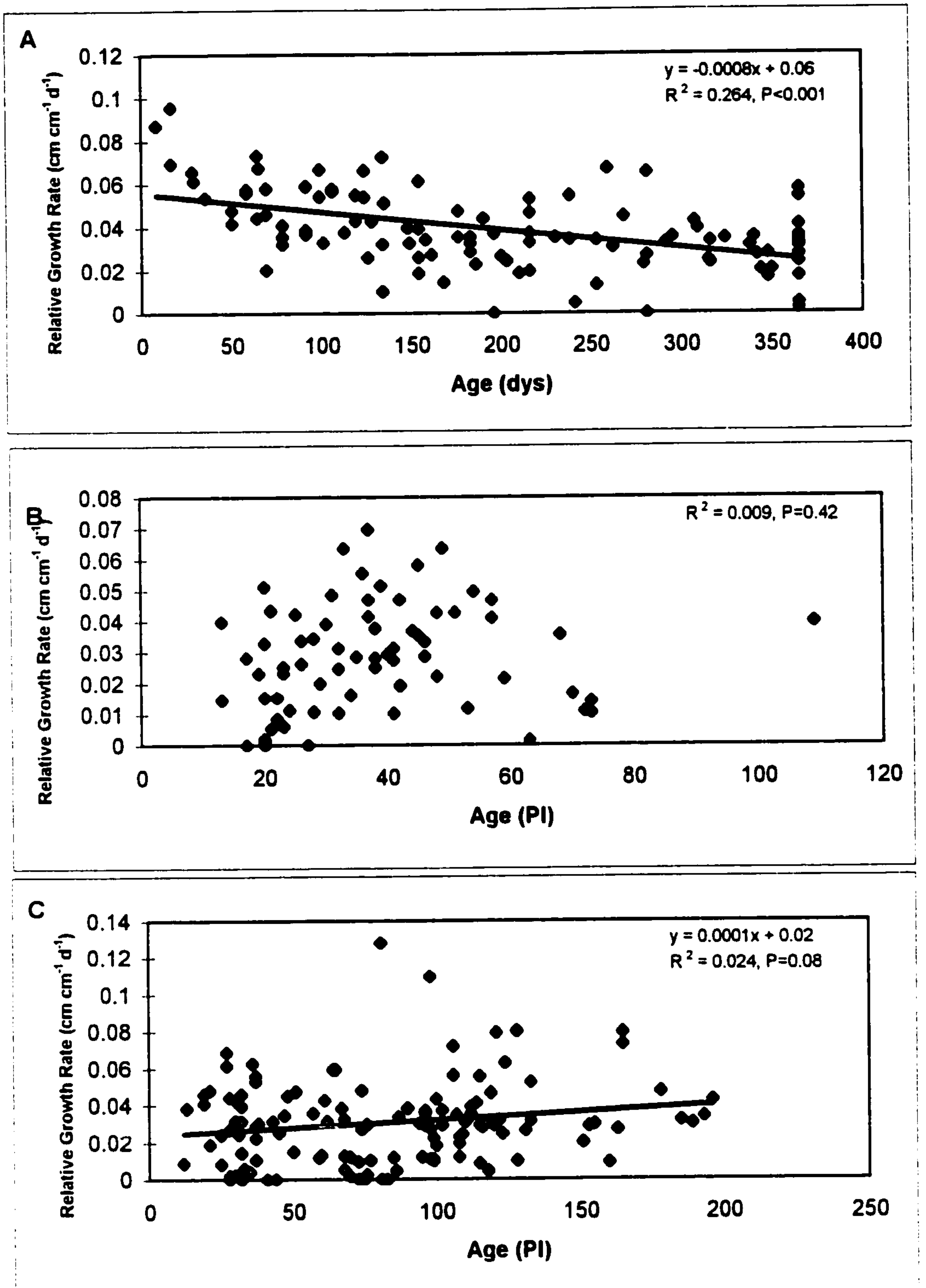
Figures 2.2A-C. Linear regressions and regression equations of maximum leaf length vs shoot age for young (< 1yr), old (mean PI = 39) and oldest (mean PI = 79) *Thalassia* shoots. Age is in chronological time for young shoots, and in PI units for old and oldest shoots. Data for young shoots are from the single sampling data set (see Section 2.3.3).



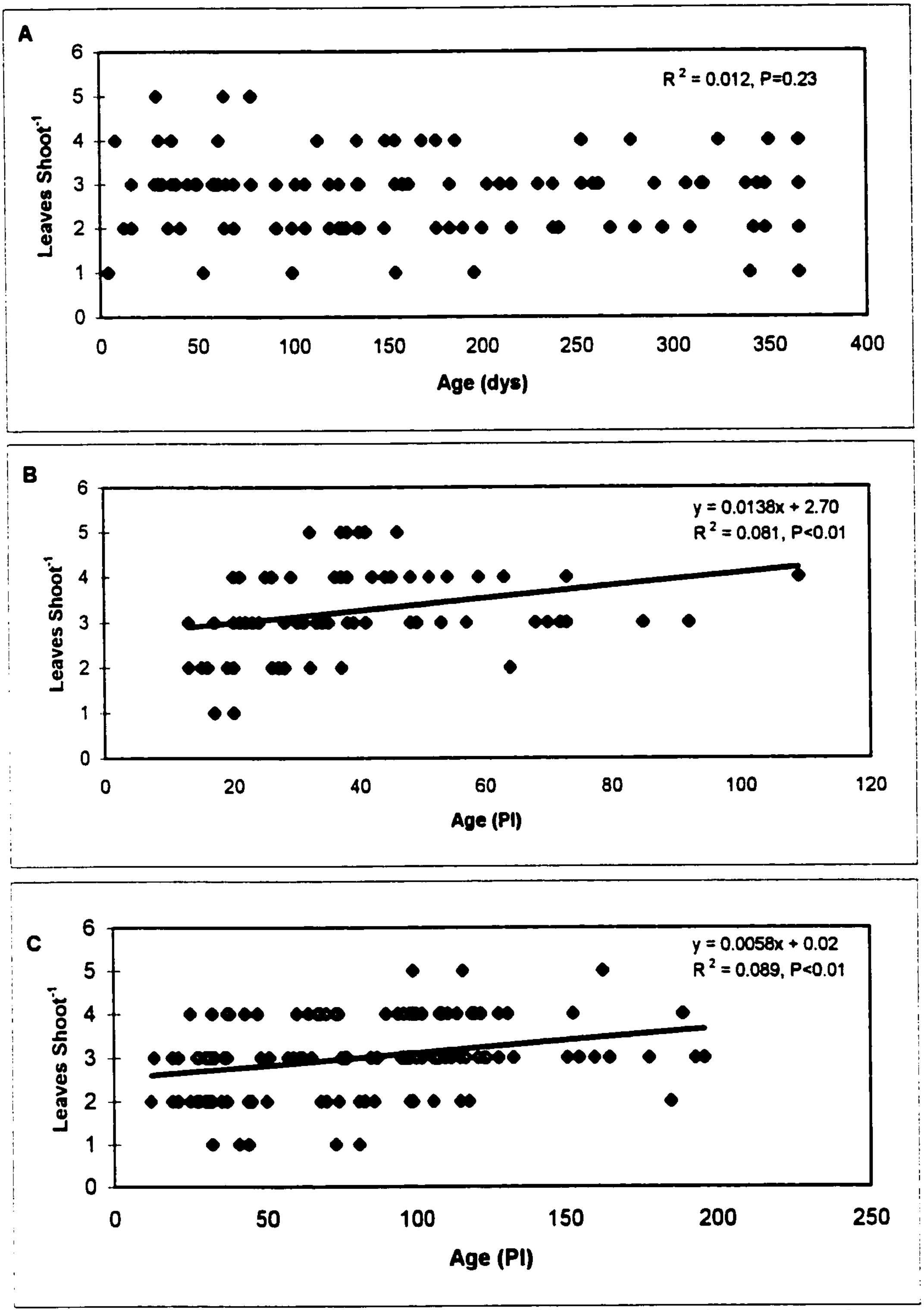
**Figures 2.3A-C. Linear regressions and regression equations of leaf width vs shoot age for young (< 1yr), old (mean PI = 39) and oldest (mean PI = 79) *Thalassia* shoots. Age is in chronological time for young shoots, and in PI units for old and oldest shoots. Data for young shoots are from the single sampling data set (see Section 2.3.3).**



Figures 2.4A-C. Linear regressions and regression equations of plastochron interval vs shoot age for young (< 1yr), old (mean PI = 39) and oldest (mean PI = 79) *Thalassia* shoots. Age is in chronological time for young shoots, and in PI units for old and oldest shoots. Data for young shoots are from the single sampling data set (see Section 2.3.3).



**Figures 2.5A-C.** Linear regressions and regression equations of relative leaf growth rate vs shoot age for young (< 1yr), old (mean PI = 39) and oldest (mean PI = 79) *Thalassia* shoots. Age is in chronological time for young shoots, and in PI units for old and oldest shoots. Data for young shoots are from the single sampling data set (see Section 2.3.3).



Figures 2.6A-C. Linear regressions and regression equations of leaves per shoot vs shoot age for young (< 1yr), old (mean PI = 39) and oldest (mean PI = 79) *Thalassia* shoots. Age is in chronological time for young shoots, and in PI units for old and oldest shoots. Data for young shoots are from the single sampling data set (see Section 2.3.3).

(Figure 2.4B; F=3.34, P=0.07). There was a significant positive relationship between shoot age and leaf width (Figure 2.3B; F=6.75, P<0.01), and between shoot age and leaves per shoot (Figure 2.6B; F=6.44, P<0.01). There was no effect of shoot age on relative leaf growth rate (Figure 2.5B; F=0.66, P=0.42).

### 2.4.2.2 *Oldest Shoots*

Shoot age also affected leaf growth variables in the oldest shoots, i.e. shoots with mean ages between 77 and 104 PI units. There was a weak positive relationship between shoot age and leaf growth rate (Figure 2.1C; Linear Regression Analysis: F=3.19, P=0.07), and between shoot age and relative leaf growth rate (Figure 2.5C; F=3.07, P=0.08). There was a significant positive relationship between shoot age and leaf width (Figure 2.3C; F=12.80, P<0.001), and between shoot age and leaves per shoot (Figure 2.6C; F=6.44, P<0.01). There was no effect of shoot age on either maximum leaf length (Figure 2.2C: F=0.56, P=0.45) or leaf PI (Figure 2.4C; F=0.73, P=0.39).

## 2.5 DISCUSSION

The only previous published study of effects of shoot age on leaf growth variables in seagrasses has been that of Duarte and Sand-Jensen (1990), who showed that leaves per shoot and leaf length increased with shoot age in *Cymodocea nodosa*. Although there have been no studies of shoot age effects on leaf growth variables in *Thalassia testudinum*, Zieman (1968) and Patriquin (1973) commented that plastochron intervals are much shorter, i.e. leaf production rates are much faster, in very young shoots. The implication is that the effect is restricted to shoots immediately after emergence, i.e. less than 1 month old (Patriquin 1973).

In the present study, effects of shoot age on leaf growth were assessed for 3 discrete age categories of shoots. The youngest age category (young shoots) was comprised of shoots less than 1 year old. The mid-age cateogry (old shoots) was comprised of shoots with a mean age of between 34 and 41 PI units. For shoots in this age category, the mean plastochron interval was about 19.8 days (see Figure 2.4B; but note that plastochron interval changes somewhat with shoot age in this age category). Using the mean plastochron interval, the mean age of these shoots in chronological time ranged from 673 to 812 days, i.e. from about 1.8 to about 2.2 years. The oldest age category (oldest shoots) was comprised of shoots with a mean age of between 77 and 104 PI units. For shoots in this age category, the mean plastochron interval was about 21.4 days (see Figure 2.4C). Using this value, the mean age of shoots in the oldest age category in chronological time ranged from 1,646 days to 2,223 days, i.e. from about 4.5 to about 6.1 years.

In this study, plastochron interval increased (i.e. rate of leaf production decreased) significantly with age for shoots less than 1 year old (Figure 2.4A). The increase in PI with age was still weakly detectable for shoots between 1.8 and 2.2 years old (Figure 2.4B), but there was no further change in PI with age for shoots between 4.5 and 6.1 years old (Figure 2.4C). The fact that PI is not constant, but decreases with age, has important implications for the use of PI to generate age-frequency distributions from which demographic predictions about *Thalassia* stands are made (the "reconstruction technique": Duarte *et al.* 1994). If young shoots have more leaf scars than they should for their true chronological age, they will be classified as older than they are, i.e. the younger age classes in an age-frequency distribution will be under-represented. This may well explain why the reconstruction technique consistently appears to predict population decline; and has done so in situations in which subsequent field work has recorded population increases (e.g. see predictions by Durako (1994) and field work of Jensen *et al.* (1996). Kaldy *et al.* (1999) emphasised that a decrease in PI with age would lead to incorrect demographic predictions for *Thalassia testudinum*, and they adjusted for this effect in generating *Thalassia* age distributions. However, adjustment may be required over a wider age range than previously envisaged, given the present results suggesting that effects of shoot age on PI may be detectable in shoots as old as 2 years.

The results of this study suggest that several leaf growth variables, apart from PI, change with shoot age. Leaf growth rate increased significantly with shoot age for shoots younger than 1 year old, and weak positive effects of shoot age on leaf growth were detectable for shoots about 2 years old, as well as for shoots between 4.5 and 6 years old (see Figures 2.1A-C). Maximum leaf length also increased significantly with shoot age for shoots younger than 1 year old (Figure 2.2A). A weak positive effect of shoot age on leaf length was still detectable for shoots around 2 years old, but the effect had disappeared for shoots between about 4.5 and 6 years old (Figures 2.2B,C). Leaf length was one of the variables reported by Duarte and Sand-Jensen (1990) to increase with shoot age in *Cymodocea nodosa*. The other leaf variable reported to increase with shoot age in *C. nodosa* is leaves per shoot (Duarte and Sand-Jensen 1990), and a similar effect was detected for mature shoots of *Thalassia testudinum* in this study. Leaves per shoot increased signficantly with shoot age for shoots about 2 years old and for those between 4.5 and 6 years old. However, the amount of variation in leaves per shoot explained by variation in shoot age was low in both cases, and shoot age did not affect leaves per shoot in *Thalassia* shoots less than 1 year old (Figures 2.6A-C). Leaf width increased significantly with shoot age in all age categories in the present study, raising the possibility that leaf width can be used as a crude predictor of shoot age in *Thalassia* (Figures 2.3A-C). However, although shoot age explained as much as 46% of the variation in leaf width in shoots less than 1 year old, it explained only about 18% of the variance in leaf width in shoots about 2 years old, and only about 9% of the leaf width variance in shoots between 4.5 and 6 years old (Figures 2.3A-C). Environmental factors may therefore be responsible for generating a considerable amount of the variation in leaf width in older *Thalassia* shoots. Indeed, studies have shown geographic variation in leaf width in *Thalassia* (McMillan 1978), and leaf width has been suggested to be an useful indicator of environmental stress in *Thalassia* (Phillips and Lewis 1983; van Tussenbroek 1996; Chapter 3 this thesis).

Relative leaf growth rate (rate at which new leaf material is added per unit of leaf material present on the shoot) decreased with increasing shoot age in *Thalassia* shoots less than 1 year old (Figure 2.5A). Two processes will affect relative leaf growth rate; the first is the rate of production of new leaves on the shoot (which decreases with shoot age in young *Thalassia* shoots; see increase in PI, Figure 2.4A), and the second is leaf growth rate (which increases with shoot age in young *Thalassia* shoots; see Figure 2.1A). The fact that relative leaf growth rate decreases with shoot age in young shoots suggests that the effect of leaf production is stronger than the effect of leaf growth rate in influencing the rate of production of new leaf material on young shoots (< 1 yr old). Interestingly, there is a trend reversal with respect to relative leaf growth rate as shoot age increases. For shoots about 2 years old, there is no effect of shoot age on relative leaf growth rate; and for shoots between 4.5 and 6 years old, there is a weak positive effect of shoot age on relative leaf growth rate (see Figures 2.5A-C for trend reversal). The positive relationship between relative leaf growth rate and shoot age in the oldest shoots is consistent with the fact that there is no effect of shoot age on rate of leaf production, but a positive effect of shoot age on leaf growth in this age category (see Figures 2.2C and 2.4C). The fact that there can be trend reversal between leaf growth variables and shoot age with increasing shoot age emphasises the need for future studies of effects of shoot age on growth variables to initially assess such effects within separate age categories.

Strong effects of shoot age on leaf growth variables were detected for young *Thalassia* shoots (< 1 yr old) in this study, with shoot age explaining significant portions of the variance observed in leaf growth. Moreover, significant effects of shoot age on leaf growth were also detected in both the 2 year old and 4.5 to 6 year old age categories. However, the amount of variance in leaf growth explained by shoot age was substantially less in these age categories than for the younger shoots. The effects of shoot age on leaf growth detected in this study clearly suggest that shoot age has been largely overlooked as a potential contributor to the considerable variation typically observed in leaf growth variables in seagrasses. For example, given the variation in age structure observed between sites in the present study, spatial variation in leaf growth variables in seagrass patches may often have a shoot age component. This may be particularly so with respect to "edge effects", i.e. shoots near the edge of seagrass patches may typically be younger than shoots farther from the edge (see Duarte and Sand-Jensen 1990). Beyond this, seasonal variation in leaf growth variables in seagrasses could theoretically have a shoot age component, if shoot recruitment was both seasonal and strong; and long-term changes in leaf growth variables may have a shoot age component, if age distributions are changing over time.

The only two studies to specifically investigate effects of shoot age on leaf growth variables in seagrasses have both detected significant effects. One of these studies (Duarte and Sand-Jensen 1990) was on the temperate species *Cymodocea nodosa* and the other (the present study) was on a tropical species *Thalassia testudinum*. This suggests that shoot age effects on leaf growth variables may be a common characteristic of seagrasses, and emphasises the need for further studies to assess the generality of these effects.

# CHAPTER 3 EFFECTS OF SHORT-TERM CHANGES IN COASTAL WATER QUALITY ON SEAGRASS ABUNDANCE AND LEAF GROWTH IN BARBADOS

## 3.1 ABSTRACT

Effects of short-term changes in coastal water quality on seagrass abundance and leaf growth were investigated in St. Lawrence Bay, Barbados by monitoring changes in response to sub-surface water being pumped into the Bay to drain an inland site adjacent to a mangrove swamp for construction purposes. The discharge lasted for 15 months, but was typically restricted to about a 4 hour period daily. Turbidity, SPM levels, nitrate concentrations and sedimentation rates were significantly higher during discharge than before discharge at the study sites, with turbidity levels being substantially in excess of recommended thresholds for seagrasses. Abundance of *Thalassia testudinum*, both as shoot density and biomass per substrate area, decreased significantly during the discharge event, as did the area-specific growth variable, productivity. These declines appear to have resulted primarily from reduced light following the increased turbidity. Negative impacts of the plume discharge were also detected on shoot-specific *Thalassia* variables, specifically leaf biomass per shoot, leaves per shoot and leaf width. Maximum leaf length, plastochron interval, and leaf growth rate did not change significantly during the discharge event, but relative leaf growth rate and specific leaf productivity rate increased during discharge. On the basis of responsiveness to environmental stress and ease of measurement, shoot density and leaf width are recommended as priority variables to include in *Thalassia* monitoring programs. The abundance of *Syringodium filiforme* increased at most sites during the discharge event, probably as a result of increased sediment nutrient availability resulting from *Thalassia* loss. The changes observed in *Thalassia* and *Syringodium* abundance support the suggestion that eutrophication can reverse the seral development of seagrass colonisation from the later species *Thalassia* to the earlier species *Syringodium*; and are consistent with the suggestion that *Thalassia* is the more

effective competitor for sediment nutrients and *Syringodium* the more effective competitor for light. Data reported in the literature suggest that the ratio of belowground biomass to aboveground biomass is higher for *Thalassia* than *Syringodium*. This may make *Thalassia* the more effective competitor for sediment nutrients by providing it with a higher capacity to obtain and store sediment nutrients per unit of total biomass to support. Conversely, the higher aboveground to belowground biomass ratio of *Syringodium* may make it the more effective light competitor by providing it with a higher capacity to obtain light per unit of total biomass to support.

## 3.2 INTRODUCTION

Seagrasses have high light requirements (Kenworthy and Haunert 1991), and are consequently restricted to shallow nearshore locations. This makes them vulnerable to land-based pollution and other anthropogenic coastal activities, and local declines in seagrass abundance in response to anthropogenic stresses have been increasingly reported (e.g. Florida, USA: Robblee *et al.* 1991, Thayer *et al.* 1994, Tomasko *et al.* 1996; Australia: Shepherd *et al.* 1989, Walker and McComb 1992; Netherlands: den Hartog and Polderman 1975; Mediterranean: Marba *et al.* 1996). Hemminga (1998) noted that more than 65% of documented declines in seagrass populations are attributable to human activities. Dredging and other physical impacts, such as anchor and propellor damage, have caused significant seagrass loss (Taylor and Salomon 1968; Zieman 1976; Onuf 1994; Sargent *et al.* 1995; Dawes *et al.* 1997), but poor water quality, including water clarity, is perhaps the most frequently cited cause of seagrass decline (Short and Wyllie-Echeverria 1996; Fonseca *et al.* 1998; Livingston *et al.* 1998). Increased quantities of sediments and nutrients (eutrophication) entering the coastal zone are the primary cause of poor water quality. Suspended solids directly reduce water clarity, and hence light availability to seagrasses, and eutrophication reduces light availability indirectly. For example, eutrophication increases algal abundance in the water column, increases algal epiphytes on seagrass leaves and increases the abundance of benthic macroalgae (Borum and Wium-Andersen 1980; Cambridge *et al.* 1986; Tomasko and Lapointe 1991). Epiphytes also impact negatively on seagrasses by reducing dissolved oxygen in the water column (van Montfrans *et al.* 1984; Twilley *et al.* 1985; Silberstein *et al.* 1986), and increasing leaf loss during wave surges (Heijs 1985; Borowitzka and Lethbridge 1986). Apart from these indirect effects of eutrophication, nitrogen enrichment has been shown to be directly toxic to the temperate seagrass *Zostera marina* (Burkholder *et al.* 1992, 1994; van Katwijk *et al.* 1997). It is important to note that, although persistent eutrophication may negatively impact seagrasses as described above, the inital response to eutrophication may often be increased growth and abundance (Powell *et al.* 1989; Fourqurean *et al.* 1995), since subtropical and tropical seagrasses typically grow in oligotrophic waters and are often nutrient-limited.

There have been no studies of anthropogenic impacts on seagrasses in the eastern Caribbean. However, there is a qualitative perception that seagrass abundance is declining in Barbados, and concern is heightened by the limited extent of seagrass beds and their close proximity to shore, by the substantial tourism-driven development that has occurred in Barbados over the last 3 decades, and by recent reports suggesting significant increases in nutrient loading of the coastal zone (Delcan 1995a; Halcrow 1998a; Wellington 1999). Nearshore coral reefs in Barbados are known to have deteriorated in recent decades, partly in response to deteriorating coastal water quality (Tomascik and Sander 1987; Allard 1993).

Eutrophication may reverse the seral development of seagrass colonisation (Lapointe *et al.* 1994; Fourqurean *et al.* 1995). The typical successional sequence for seagrass communities in the Caribbean is colonisation of substrata by rhizophytic green macroalgae, followed by the seagrasses *Halodule wrightii* and/or *Syringodium filiforme*, and ending with *Thalassia testudinum* (den Hartog 1971; Zieman 1976; Williams 1987, 1990). The general consensus is that early colonisers precede later colonisers because they have faster leaf and rhizome growth and are therefore more adept at colonising open space (Gallegos *et al.* 1994), and because they are more tolerant of unstable substrates (den Hartog 1971; Patriquin 1975). Later colonisers are suggested to replace earlier colonisers primarily because they are more effective competitors for sediment nutrients (Williams 1990 for *Thalassia*'s replacement of *Syringodium*; Fourqurean *et al.* 1995 for *Thalassia*'s replacement of *Halodule*). Fourqurean *et al.* (1995) suggest that it is because earlier colonisers have higher nutrient demands that later colonisers can reduce sediment nutrients below the levels required by the former. Williams (1990) suggests that *Syringodium*'s replacement by *Thalassia* is aided by the latter being also the better competitor for light.

The suggestion of Lapointe *et al.* (1994) and Fourqurean *et al.* (1995) that eutrophication reverses colonisation sequence is based on their documenting increased abundance of the earlier coloniser *Halodule wrightii* and decreased abundance of the later coloniser *Thalassia testudinum* in the Florida Keys and in Florida Bay in response to eutrophication. The increased abundance of *Halodule* is expected as a response to the increased availability of sediment nutrients. The cause of the decreased abundance of *Thalassia* is less clear. Lapointe *et al.* (1994) suggest that it results from increased biomass of attached epiphytes and macroalgae, which attenuate light and reduce dissolved oxygen; the implication is that these factors are less detrimental to *Halodule*. Fourqurean *et al.* (1995) suggest that the decrease in *Thalassia* abundance results from direct competition between *Thalassia* and *Halodule* for light, with the latter having the lower light requirement and being the more effective light competitor. This suggestion differs from the position of Williams (1987,1990) who suggested that *Thalassia*'s dominance in seagrass communities results from its ability to outcompete *Halodule* and *Syringodium* for both sediment nutrients and light. Whether eutrophication results in reversal of seagrass seral development from *Thalassia* to *Syringodium* has not been investigated.

Sediment accretion may also reverse the seral development of seagrass colonisation, i.e. it may increase the abundance of *Halodule* and *Syringodium* relative to *Thalassia*. *Halodule* and *Syringodium* have higher shoot turnover rates than *Thalassia*, which allows them to better adjust to changes in the sediment surface, and thereby decreases their susceptibility to sediment accretion and burial (Williams 1990; Fourqurean *et al.* 1995; Woodward-Clyde 1998). Moreover, the higher rhizome growth rate of these species allows them to colonise new space created by sediment accretion more rapidly than *Thalassia* (Gallegos *et al.* 1994). Duarte *et al.* (1997) showed sharp reductions in shoot density in response to sediment burial in *Thalassia hemprichii*, a closely related species to *T. testudinum*, and an initial decrease in shoot densities of *Halodule wrightii* and *Syringodium iseotifolium*, followed by a subsequent recovery.

One consequence of the seagrass losses that are occurring worldwide is an increasing need to identify seagrass variables that may be useful indices of the ecological condition of existing beds, but studies aimed at identifying eco-indicators are rare (but see Durako 1995; Lee and Dunton 1997). Despite the warning by Fonseca *et al.* (1998) that morphological characteristics of seagrasses are likely to be only loosely linked to functional characteristics of seagrass beds, it would seem appropriate to seize opportunities in which seagrasses are undergoing rapid abundance losses to attempt to identify whether there are shoot-specific characteristics which change when abundance losses are occurring, and which may therefore be viewed as useful indicators of the condition of seagrass beds.

In 1996, construction of a sewage treatment facility began near the periphery of a mangrove swamp inland of a seagrass site at St. Lawrence, Barbados. The swampy nature of the area required the construction site to be drained. The underlying water was pumped into an adjacent mangrove pond, and discharged via a sluice gate into St. Lawrence Bay. It is estimated that at least 500,000-750,000 gallons of the water were pumped daily into the pond for subsequent discharge to the Bay. The pumping and discharge lasted for 15 months. Discharge to the Bay occurred almost daily throughout this period, but was typically restricted to about a 4-hour period in the morning (i.e. before noon). This situation created an unique opportunity to investigate the effects of water quality changes, as they were occurring, on seagrasses in St. Lawrence Bay.

The objectives of this Chapter are therefore (1) to document changes in abundance and growth variables of *Thalassia testudinum* in St. Lawrence Bay during the discharge event described above, and to comment on their value as indicators of seagrass vitality (eco-indicators); (2) to investigate changes in abundance of *Syringodium filiforme* during the discharge event; (3) through (1) and (2), to comment on whether water quality changes can reverse the seral development of seagrass beds from *Thalassia* to *Syringodium*; and (4) to characterise the water quality changes which occurred at the seagrass sites in St. Lawrence Bay in response to the discharge event, and identify which water quality components may have been most important in influencing the seagrass changes observed.

## 3.3 METHODS

### 3.3.1 Locations and Characteristics of Sampling Sites

The study was conducted at St. Lawrence, on the south coast of Barbados (see Chapter 1, Section 1.3 for location and description of the St. Lawrence site). The pumping of water to drain the construction site, and its subsequent discharge into St. Lawrence Bay, began in March 1996 and was completed in May 1997. Data were collected from 8 sites in St. Lawrence Bay. Each of the sites consisted of a permanently established 1 $m^2$ area. The locations of the 8 sites were chosen to generate variation in distance of the sites from the discharge point of the water into St. Lawrence Bay, and in likely impacts of the discharged water on seagrasses at the sites. Preliminary work with surface current drogues had indicated that the likely direction of travel of the discharge plume from the discharge point would be west-northwest, i.e. along the coastline towards the west (see Figure 3.1). The locations of the 8 sites in relation to the discharge point are shown in Figure 3.1. Once discharge had commenced, it could be visually confirmed that the typical direction of plume travel was initially south-west driven by the velocity of discharge, and then west-northwest driven by the prevailing currents. The frequency with which the plume actually passed over each of the 8 sites was monitored during the study by simply recording, at either the beginning or end of most morning sampling occasions, which sites the plume was passing over. This produced a contact probability of the plume with the site for each site. The product of this contact probability and the inverse of the distance between the plume discharge point and the site was used to calculate an impact index for each site. The depth of each site (MLW; mean low water), its distance from the plume discharge point, the measured contact probability of the plume with the site, the calculated impact index of the plume on the site, and a calculated daily contact duration of the plume with the site (based on the contact probability of the plume with the site and the typical 4 hour duration of daily plume discharge), are shown in Table 3.1. Site 3 was clearly the least affected site, with the plume only being observed to pass over this site on two occasions during the study.

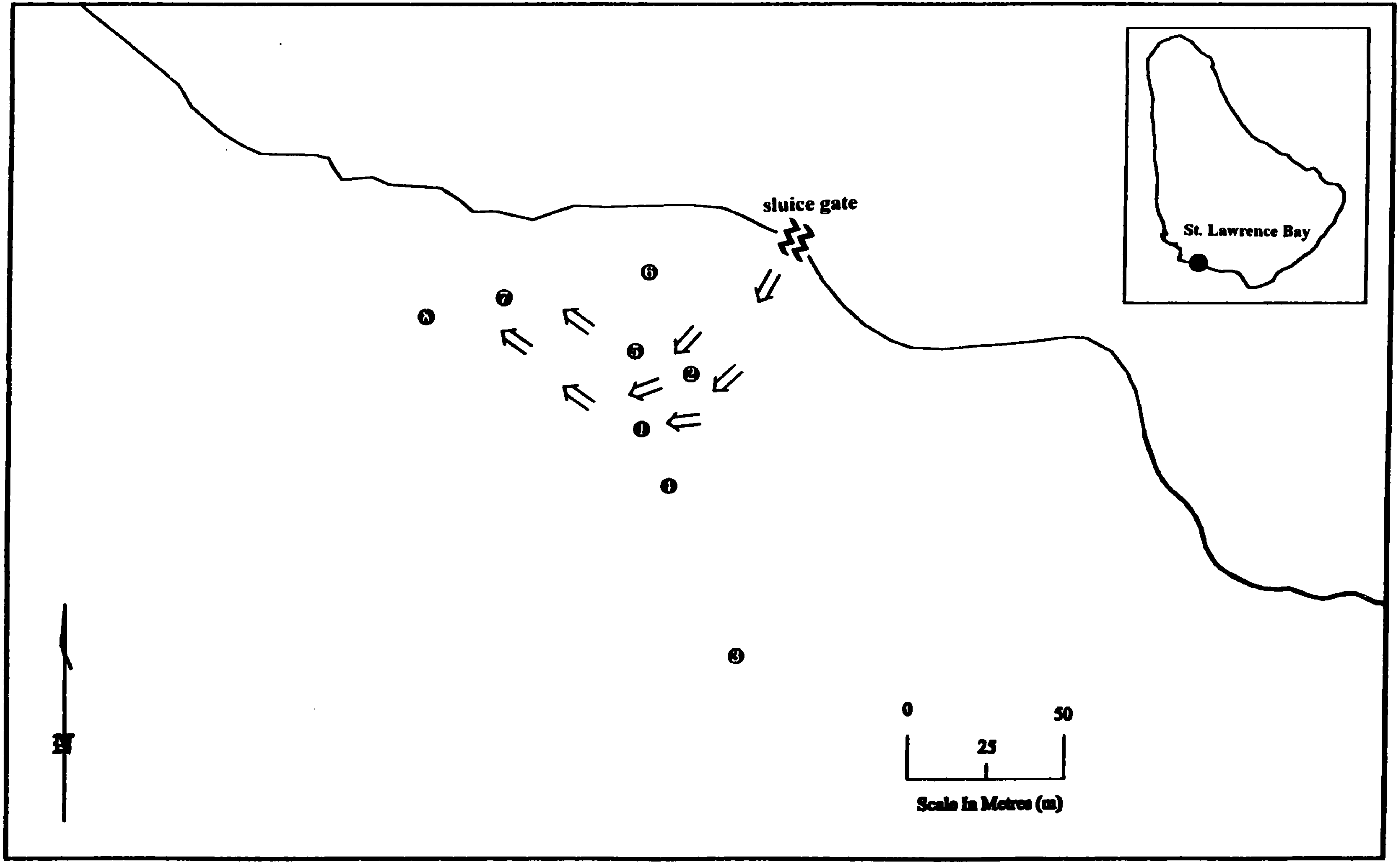


Figure 1. Locations of study sites in St. Lawrence Bay in relation to the sluice gate through which the plume was discharged. Arrows indicate general direction of typical plume travel.

**Table 3.1.** Depth (m; MLW), distance from plume discharge point (m), plume contact probability (%), plume impact index (%), and calculated plume contact duration (hrs) for each study site. Calculation of variables as described in Methods.

| Site | Depth | Distance | Contact Probability | Impact Index | Contact Duration |
|---|---|---|---|---|---|
| 1 | 0.5 | 75 | 80 | 1.07 | 3.2 |
| 2 | 0.5 | 67 | 100 | 1.49 | 4.0 |
| 3 | 0.7 | 130 | 5 | 0.04 | 0.2 |
| 4 | 0.7 | 90 | 50 | 0.56 | 2.0 |
| 5 | 0.7 | 60 | 70 | 1.17 | 2.8 |
| 6 | 0.6 | 45 | 50 | 1.11 | 2.0 |
| 7 | 1.0 | 88 | 80 | 0.91 | 3.2 |
| 8 | 1.2 | 116 | 60 | 0.52 | 2.4 |

### 3.3.2 Measurements of Abundance and Growth

Data on abundance and leaf growth of *Thalassia testudinum*, on biomass of fleshy epiphytes on *Thalassia* leaves, and on *Syringodium* abundance were collected from the 8 permanently located 1 $m^2$ sites in the month prior to discharge (Februrary 1996), in 3 months during discharge (May and October 1996, February 1997), in the month in which discharge ceased (May 1997), and 5 months following discharge cessation (October 1997). On each sampling occasion, a different 25 cm x 25 cm (0.0625 $m^2$) quadrat was randomly selected in each 1 $m^2$ sampling site, and the abundance and leaf growth variables were measured using all shoots in the quadrat. Different shoots were therefore measured on each sampling occasion, ensuring that comparisons between sampling occasions (e.g. February 1996 to February 1997 and February 1996 to May 1997) were independent of each other. The decision to measure shoots within 25 cm x 25 cm quadrats was made following *a priori* sampling which indicated no difference in sample variances between shoots randomly selected within the quadrats and shoots randomly selected across the study area.

The *Thalassia* abundance variables measured were shoot density and leaf biomass (as biomass per shoot, and as biomass per unit substrate area). The *Thalassia* leaf growth variables measured were average leaf growth rate per shoot, relative leaf growth rate per shoot, maximum leaf length, leaf width, leaves per shoot, plastochron interval (PI), leaf productivity and specific leaf productivity rate (see Chapter 1, Section 1.3 for definitions of variables and measurement details). Biomass of fleshy epiphytes on *Thalassia* leaves were measured by scraping the epiphytes off all leaves harvested from each quadrat on each sampling occasion, and drying for 24 hours at 70 °C. Epiphyte biomass was expressed as a % of dry weight leaf biomass. Abundance of *Syringodium* was measured *in situ* as number of shoots in each quadrat, and was expressed as number per $m^2$ (shoot density).

### 3.3.3 Measurements of Environmental Variables

Measurements of chlorohyll-*a*, nitrates (as $NO_3$-N), phosphates (as $PO_4$-P), suspended solids (SPM), salinity, turbidity and color were taken at 6 of the 8 permanently located 1 $m^2$ sites (Sites 1, 2, 3, 5, 6, 8), as well as at an inshore site immediately adjacent to the plume discharge point. Samples were taken on one occasion in the pre-discharge period (February 1996) at each site. Samples were also taken on one occasion at each site during the discharge period, with sampling taking place when the plume was actually passing over the site. For most sites (1, 2, 5, 6), the discharge samples were taken in February 1997. For site 8, the discharge samples were taken in March 1997, since the plume was not observed to pass over the site in February. Site 3 samples were taken in April 1997, since both occasions on which the plume was observed to pass over this site were in this month. Five samples were collected on each sampling occasion at each site. The samples were collected using 1 *l* acid-washed plastic Nalgene bottles, and stored on ice in insulated styrofoam containers immediately following collection. All analyses began within 4 hours of collection. Nitrates, phosphates, SPM and chl-*a* were analysed in accordance with the procedures described in *Standard Methods for the Examination of Waste and Wastewater* (16th Edition, 1986), based on the methods of Strickland and Parsons (1972). Twenty percent of all analyses were replicated in the laboratory for quality assurance and control.

Sedimentation rates were measured at each of the 8 sites during discharge (March-May 1997) and after discharge (June-October 1997), by placing sediment traps consisting of a PVC pipe (4.4 cm diameter) set in cement blocks at each site. One trap was set per site, and the traps were retrieved 1 week after deployment. Accumulated sediment was dried at 70 °C for 24-48 hours and weighed to give a sedimentation rate in g DW sediment $m^{-2}d$. Ash-free dry weights of samples were determined by ashing sediments in a muffle oven at 425 °C for 24 hours. Percent organic content of each sediment sample could then be determined as the difference in sediment sample dry weight and ash-free dry weight.

### 3.3.4 Data Analysis

Data were tested for normality using a one-way Kolmogorov-Smirnov test, and for homogeneity of variance using Levene's test, and were natural log transformed where necessary for parametric statistical analyses. Average leaf growth rate, relative leaf growth rate, leaf length, leaf width, and all environmental variables required transformation prior to analysis.

Principal Components Analysis (PCA) was used to examine the associations of the different *Thalassia* abundance and growth variables across the 8 sampling sites, as well as their associations with the environmental variables, before and during (at least 12 months after onset) the discharge event. This allowed determination of whether the associations between the variables differed before and during the event, and hence whether the seagrass variables appeared to differ in their response to the event, and which environmental variables appeared to be associated with the seagrass changes observed. The principal components were rotated orthogonally to facilitate the interpretations of the associations both before and after the event.

Effects of the discharge event on the growth and abundance variables, as well as on the environmental variables, were then investigated separately for each variable using paired-sample tests and analyses of variance. The effects were assessed by comparing the variables in February 1996 with February 1997 (i.e. before discharge and 1 year after discharge to control for effects of season); in February 1996 with May 1997 (i.e. before discharge and in the month when discharge ceased to assess the full impact of the discharge event); and in May 1997 with October 1997 (i.e. to assess recovery following the discharge event). All *Thalassia* abundance variables (shoot density, leaf biomass per substrate area, leaf biomass per shoot), some *Thalassia* growth variables (PI, leaf productivity, specific leaf productivity rate), as well as fleshy epiphyte biomass and *Syringodium* shoot density provided only one value per site per sampling occasion. Paired-Sample t-tests, paired by site, were therefore used to compare differences in these variables before, during and after the discharge event. For the remaining *Thalassia* growth variables (average leaf growth rate, relative leaf growth rate, maximum leaf length, leaf width and leaves per shoot), two-way analyses of variance (ANOVAs) were used to compare differences in the variables before, during and after the discharge event; and two-way ANOVAs were also used to compare the environmental variables before and during the event. To achieve a balanced statistical design, the measurements from 20 randomly selected shoots were used in the analysis of these variables. Sampling occasion (i.e. February 1996 - February 1997, February 1996 - May 1997, May - October 1997) was treated as a fixed factor and site a random factor, and Type III sums of squares were used to calculate F-values. Linear regression analyses were used to examine the relationships between percent changes in variables at each site and the plume impact index for the site.

## 3.4 RESULTS

### 3.4.1 Changes in Associations of Growth, Abundance and Environmental Variables

#### 3.4.1.1 *Associations before Discharge*

The principal components ordination biplot for the PCA conducted on the growth, abundance and environmental data collected before the discharge event is shown in Figure 3.2. The first 2 components explained 56 % of the variance in the data set. The first component had high negative loadings on the 2 area-specific *Thalassia* abundance variables, shoot density and biomass per substrate area, indicating that these variables were strongly associated across the sampling sites (Figure 3.2). The first component also loaded negatively on the area-specific *Thalassia* growth variable productivity. The first component loaded positively on the shoot-specific growth and abundance variables, leaf growth rate, relative leaf growth rate, biomass per shoot and leaves per shoot. This indicates that sites of high area-specific *Thalassia* abundance tend to have low shoot-specific growth. The first component had a high positive loading on *Syringodium* shoot density (Figure 3.2), perhaps indicating interspecific competition between *Syringodium* and *Thalassia*. The second component had a high positive loading on *Thalassia* productivity and on specific leaf productivity rate, and a high negative loading on PI, indicating that productivity is high when leaf production is rapid (Figure 3.2).

The PCA indicated little association among the environmental variables before discharge (Figure 3.2). For example, the second principal component had a high positive loading on phosphate concentration, only a weak positive loading on chlorophyll-*a*, and a strong negative loading on nitrate concentration. Moreover, the environmental variables showed little association with the *Thalassia* variables, suggesting that effects of variation in the environmental variables on *Thalassia* abundance and growth prior to discharge were small. For example, the fact that turbidity was clustered with area-specific *Thalassia* abundance

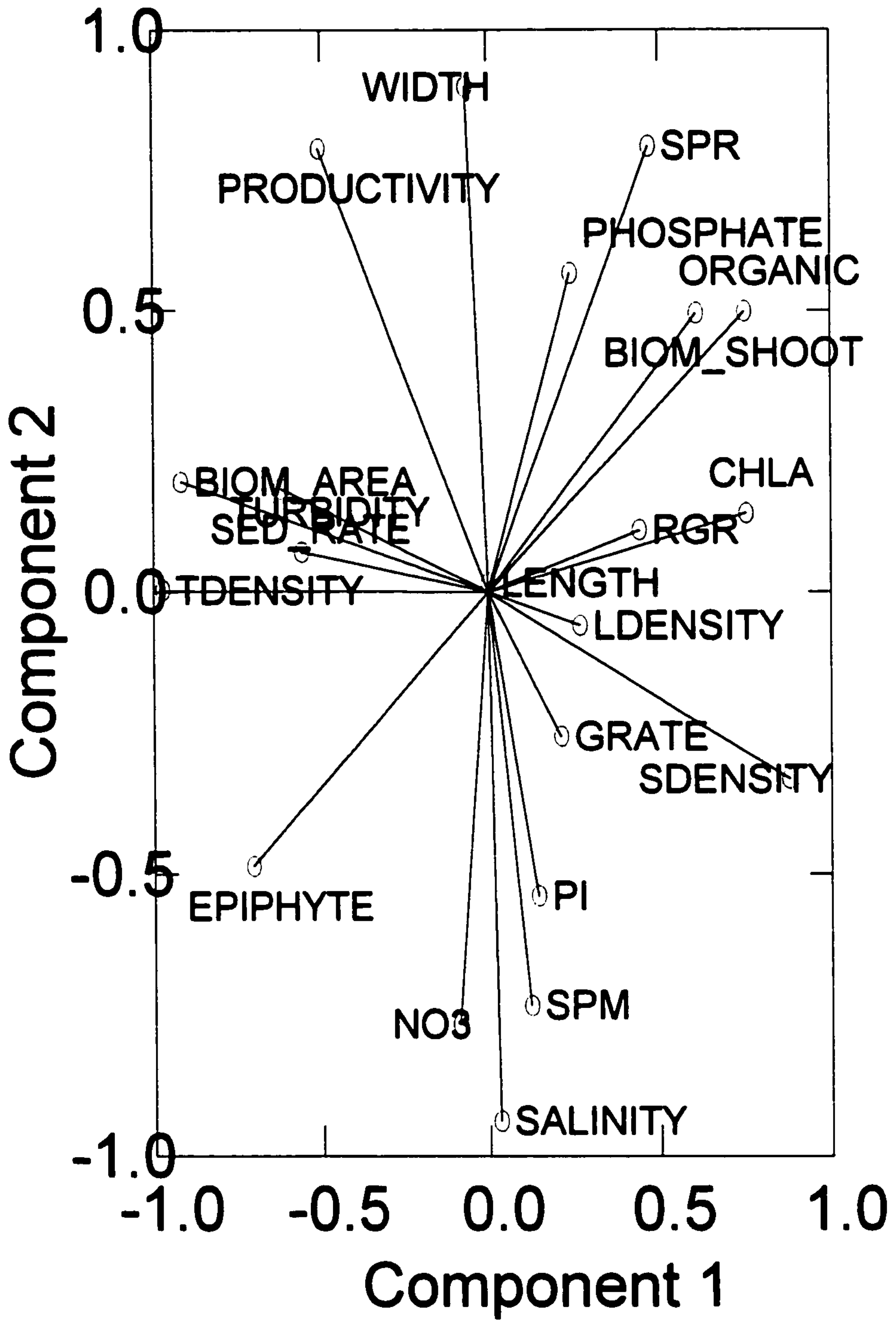


**Figure 3.2.** Principal Components Analysis ordination biplot of seagrass growth and abundance data, and environmental data, prior to the discharge event. *Thalassia* growth variables are: grate - average leaf growth rate; rgr - relative leaf growth rate; ldensity - leaves per shoot; length - leaf length; width - leaf width; productivity - leaf productivity; spr - specific leaf productivity rate, PI - plastochron interval. *Thalassia* abundance variables are: tdensity - shoot density; biom_area - biomass per substrate area; biom_shoot - biomass per shoot; sdensity - *Syringodium* shoot density; epiphyte - fleshy epiphyte biomass. Environmental variables are: NO3 - nitrates; PO4 - phosphates; chla - chlorophyll-*a*; SPM - suspended particulate matter; sed_rate - sedimentation rate; organic - sediment organic content.

(Figure 3.2) suggests that, at the levels prevailing prior to discharge, turbidity was not negatively affecting abundance. Epiphyte biomass on *Thalassia* leaves was not strongly associated with either environmental variables or *Thalassia* variables prior to discharge (Figure 3.2).

### 3.4.1.2 *Associations during Discharge*

The principal components ordination biplot for the PCA conducted on the growth, abundance and environmental data collected towards the end of the discharge event is shown in Figure 3.3. The first 2 components explained 63 % of the variance in the data set. The second component had high positive loadings on the 2 area-specific *Thalassia* abundance variables, shoot density and biomass per substrate, and on the area-specific growth variable, productivity, indicating that these variables remained strongly associated across the sampling sites during discharge. The second component had a high negative loading on leaf growth rate, again indicating that areas of high area-specific *Thalassia* abundance are not areas of high *Thalassia* leaf growth. Leaf growth and relative leaf growth, which were positively associated before discharge (Figure 3.2), were negatively associated during discharge (Figure 3.3), indicating that the discharge event had different effects on the 2 growth variables. The second component had a strong negative loading on *Syringodium* shoot density (contrast its positive loading on *Thalassia* abundance), reinforcing the suggestion of interspecific competition between *Syringodium* and *Thalassia*.

The PCA indicated much stronger association between the environmental variables during discharge (Figure 3.3) than before discharge (Figure 3.2). During discharge, the first component had strong positive loadings on all water quality variables except salinity, producing a particularly strong assocation between SPM levels and turbidity, and between nitrates, phosphates and chlorophyll-*a* (Figure 3.3). The negative association between salinity and these 3 variables is expected, in that the discharge plume should be both less saline and

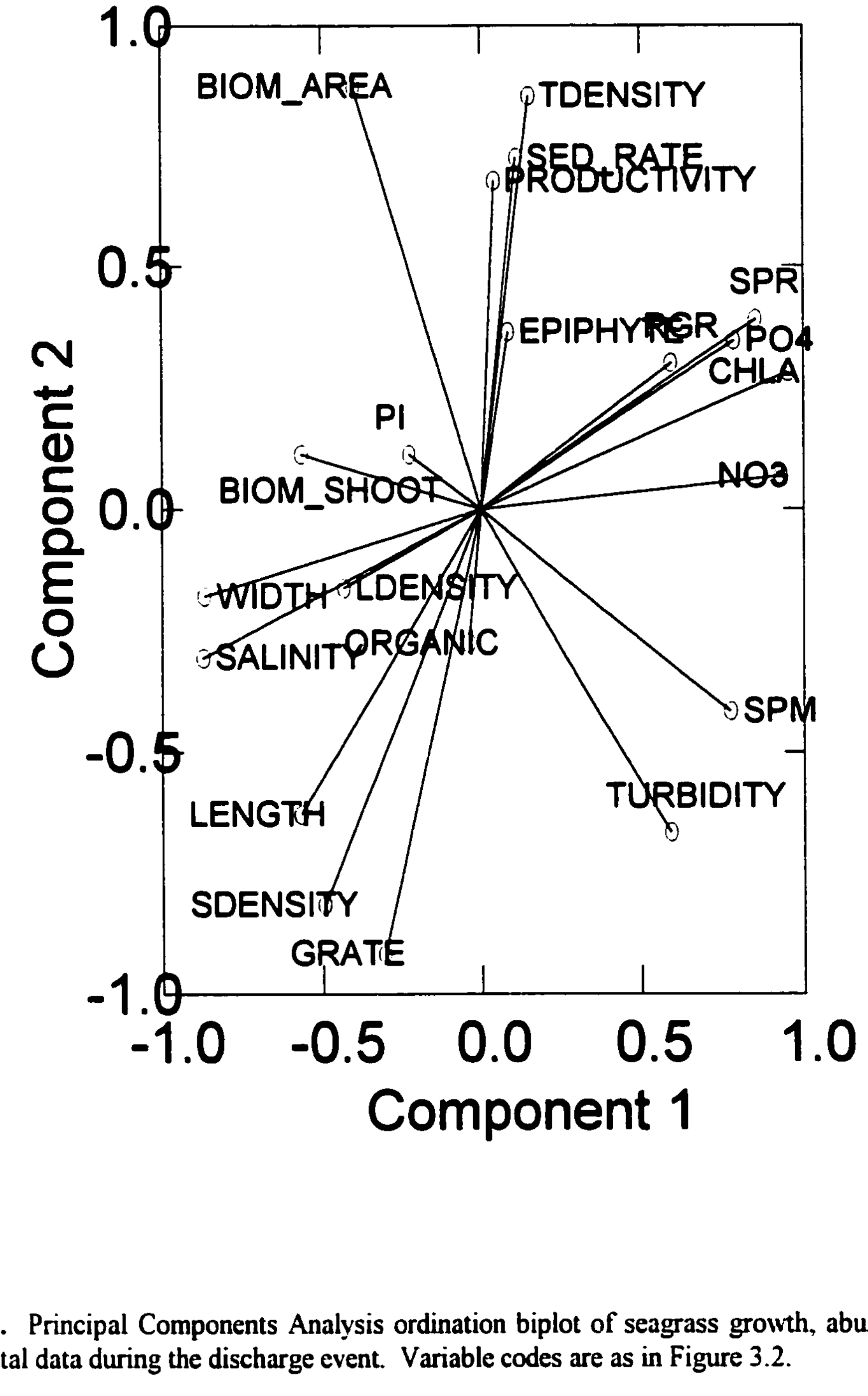


Figure 3.3. Principal Components Analysis ordination biplot of seagrass growth, abundance and environmental data during the discharge event. Variable codes are as in Figure 3.2.

more nutrient rich than the typical seawater in the Bay.

The PCA also indicated better association between the environmental variables and the *Thalassia* variables during discharge (Figure 3.3) than before discharge (Figure 3.2), suggesting that the environmental variables were affecting *Thalassia* growth and abundance following discharge. For example, Component 1 loaded positively on most environmental variables and loaded negatively on most *Thalassia* variables, suggesting a general negative effect of the environmental variables on the *Thalassia* variables. More specifically, and most noticeably, there was a strong negative association between the *Thalassia* area-specific variables (shoot density, biomass per substrate area, productivity) and turbidity and SPM levels. It should be noted that, in contrast to the situation with the other *Thalassia* variables, Component 1 had a positive loading on relative leaf growth rate and on the related variable specific leaf productivity rate, resulting in a close association of these variables with nutrient levels and chlorophyll-*a*. This supports the suggestion that relative growth rate and specific leaf productivity rate behaved differently than the other growth variables in response to the discharge event.

### 3.4.2 Changes in Individual Growth, Abundance and Environmental Variables

#### 3.4.2.1 *Changes in Thalassia Abundance*

*Shoot Density*

Changes in *Thalassia* shoot density at the 8 sites before, during and after the discharge event are shown in Table 3.2. Shoot densities declined at 7 of the 8 sites between February 1996 and February 1997 (i.e. after 1 year of discharge), and declined at all 8 sites between February 1996 and May 1997 (i.e. by the end of discharge). For all sites combined, shoot densities were significantly lower in February 1997 than February 1996 (Paired-Sample t-

**Table 3.2.** *Thalassia* shoot densities (shoots $m^{-2}$) at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996 - May 1997) and after (October 1997) the discharge event. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | SITES | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 1240 | 1168 | 704 | 288 | 584 | 864 | 688 | 720 |
| May-96 | 1168 | 820 | 676 | 240 | 560 | 766 | 672 | 624 |
| Oct-96 | 1032 | 744 | 644 | 252 | 386 | 560 | 580 | 400 |
| Feb-97 | 576 (-53.5) | 704 (-39.7) | 810 (15.1) | 240 (-16.7) | 272 (-53.4) | 576 (-33.3) | 560 (-18.6) | 404 (-43.9) |
| May-97 | 608 (-51.0) | 580 (-50.3) | 592 (-15.9) | 208 (-27.8) | 304 (-47.9) | 508 (-41.2) | 464 (-32.6) | 452 (-37.2) |
| Oct-97 | 832 (36.8) | 816 (40.7) | 608 (2.7) | 256 (23.1) | 384 (26.3) | 812 (59.8) | 528 (13.8) | 564 (24.8) |

tests paired by site: t=3.10, P<0.02); and were significantly lower in May 1997 than February 1996 (t=4.50, P<0.003). Shoot densities increased at all sites following cessation of discharge (i.e. between May 1997 and October 1997, Table 3.2); for all sites combined, the increase was statistically significant (t=3.65, P<0.01).

Plots of percent reduction in shoot density at each site versus the impact index for the site (see Methods and Table 3.1 for calculation of impact index) are shown for the losses between February 1996 and February 1997, and between February 1996 and May 1997, in Figures 3.4A and 3.4B respectively. Percent loss in shoot density increased with the impact index in both cases (Figures 3.4A,B).

### *Biomass per Shoot*

Changes in *Thalassia* biomass per shoot (g DW shoot$^{-1}$) are shown in Table 3.3. Biomass per shoot declined at all 8 sites between February 1996 and February 1997, and at all 8 sites between February 1996 and May 1997. For all sites combined, biomass per shoot was significantly lower in February 1997 than February 1996 (Paired-Sample t-tests, paired by site: t=4.02, P<0.005), and was significantly lower in May 1997 than February 1996 (t=6.35, P<0.001). Biomass per shoot increased at 6 of the 8 sites following cessation of discharge (i.e. May 1997 to October 1997; Table 3.3). For all sites combined, differences in biomass per shoot between May 1997 and October 1997 were not statistically significant (t=0.54, P=0.61).

Plots of percent reduction in biomass per shoot at each site versus the impact index at the site are shown for the losses bewteen February 1996 and February 1997, and between February 1996 and May 1997 in Figures 3.5A and 3.5B respectively. Percent reduction in biomass per shoot was not significantly correlated with the impact index in either case (Figures 3.5A,B).

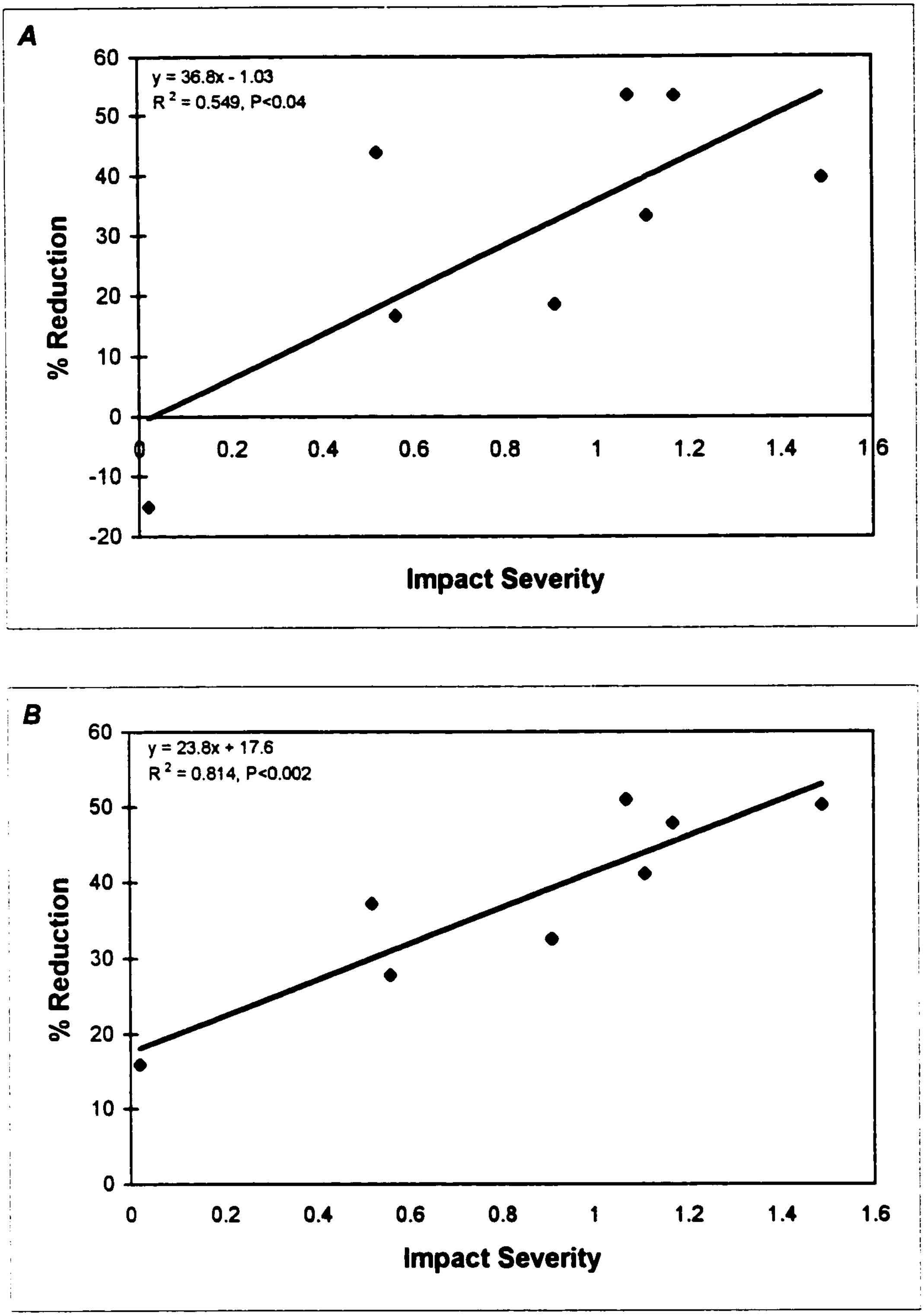


**Figure 3.4. Percent reduction in *Thalassia* shoot density (shoots $m^{-2}$) at each site versus the plume discharge impact index for the site between (A) February 1996 - February 1997, and (B) February 1996 - May 1997.**

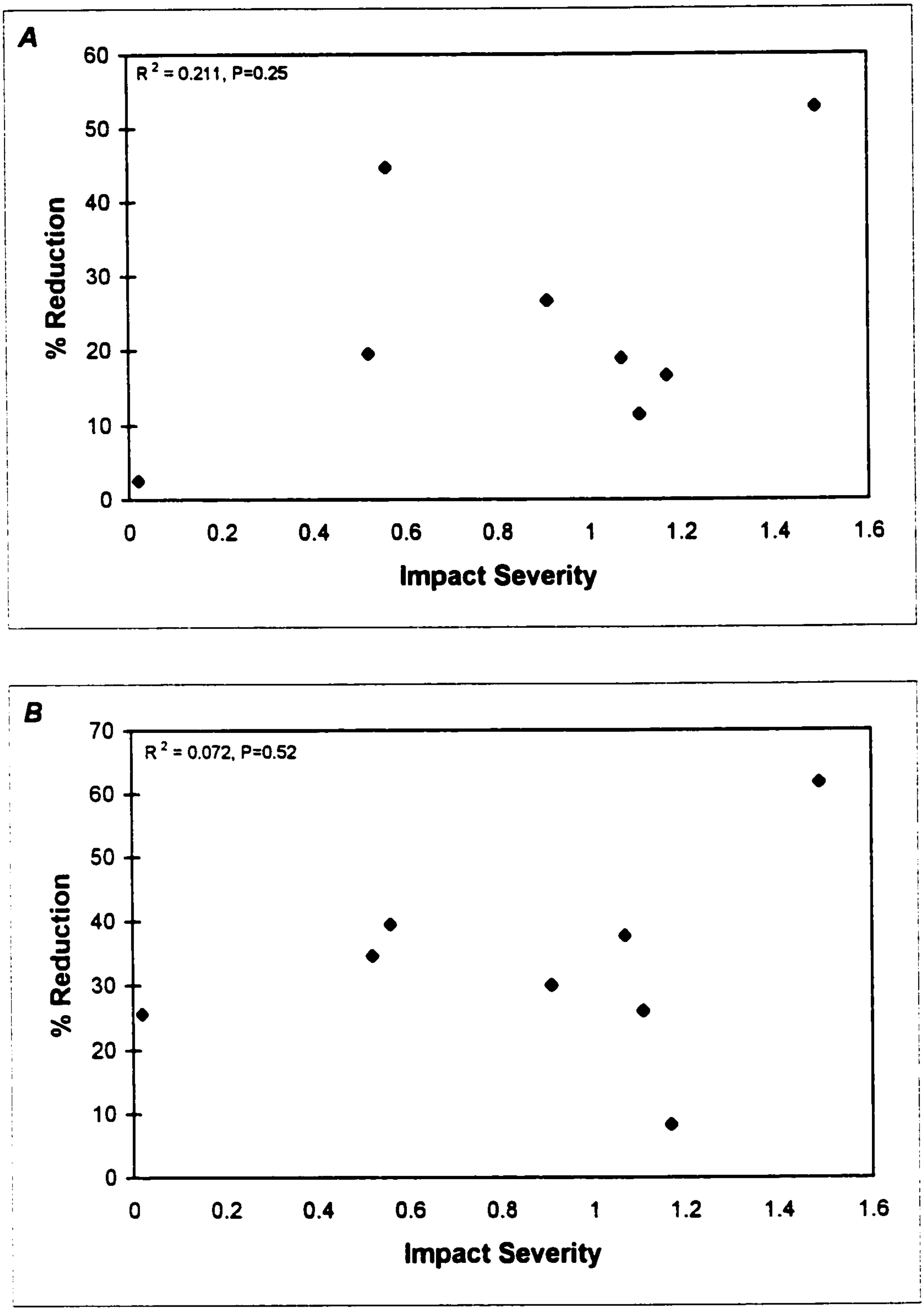


**Figure 3.5.** Percent reduction in *Thalassia* biomass per shoot (g DW shoot$^{-2}$) at each site versus the plume discharge impact index for the site between (A) February 1996 - February 1997, and (B) February 1996 - May 1997.

*Biomass per Substrate Area*

Changes in *Thalassia* biomass per substrate area (g DW $m^{-2}$) are shown in Table 3.4. Biomass declined at 7 of the 8 sites between February 1996 and February 1997, and at all 8 sites between February 1996 and May 1997. For all sites combined, biomass was significantly lower in February 1997 than February 1996 (Paired-Sample t-test, paired by site: $t=3.46$, $P<0.01$), and significantly lower in May 1997 than February 1996 ($t=5.14$, $P<0.001$). Biomass increased at 6 of the 8 sites following cessation of discharge (i.e. between May 1997 and October 1997, Table 3.4); for all sites combined, the increase was statistically significant ($t=2.45$, $P<0.05$).

Plots of percent reduction in biomass at each site versus the impact index for the site are shown for the losses between February 1996 and February 1997, and between February 1996 and May 1997, in Figures 3.6A and 3.6B respectively. Percent loss in biomass increased with the impact index in both cases (Figures 3.6A,B).

### 3.4.2.2 *Changes in Thalassia Leaf Growth*

*Leaf Productivity*

Changes in *Thalassia* leaf productivity (g DW $m^{-2}$ $d^{-1}$) at the 8 sites before, during and after the discharge event are shown in Table 3.5. Productivity declined at 7 of the 8 sites between February 1996 and February 1997, and declined at all 8 sites between February 1996 and May 1997. For all sites combined, productivity was significantly lower in February 1997 than February 1996 (Paired-Sample t-test; $t=4.10$, $P<0.005$), and was significantly lower in May 1997 than February 1996 ($t=5.18$, $P<0.001$). Productivity increased at 7 of the 8 sites following cessation of discharge (i.e. between May 1997 and October 1997; Table 3.5), but the difference between May and October was not statistically significant ($t=1.73$, $P=0.13$).

**Table 3.4.** *Thalassia* biomass per substrate area (g DW $m^{-2}$) at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | SITES | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 398 | 397 | 275 | 109 | 210 | 334 | 206 | 269 |
| May-96 | 362 | 262 | 237 | 84 | 202 | 245 | 161 | 243 |
| Oct-96 | 227 | 134 | 167 | 66 | 85 | 168 | 110 | 140 |
| Feb-97 | 150 (-62.3) | 113 (-71.5) | 308 (12.0) | 50 (-54.1) | 82 (-61.0) | 197 (-41.0) | 123 (-40.3) | 121 (-55.0) |
| May-97 | 122 (-69.3) | 75 (-81.1) | 172 (-37.5) | 48 (-56.0) | 100 (-52.4) | 145 (-56.6) | 97 (-52.9) | 110 (-59.1) |
| Oct-97 | 194 (59.0) | 114 (52.0) | 158 (-8.1) | 90 (87.5) | 81 (-19.0) | 260 (79.3) | 116 (19.6) | 165 (50.0) |

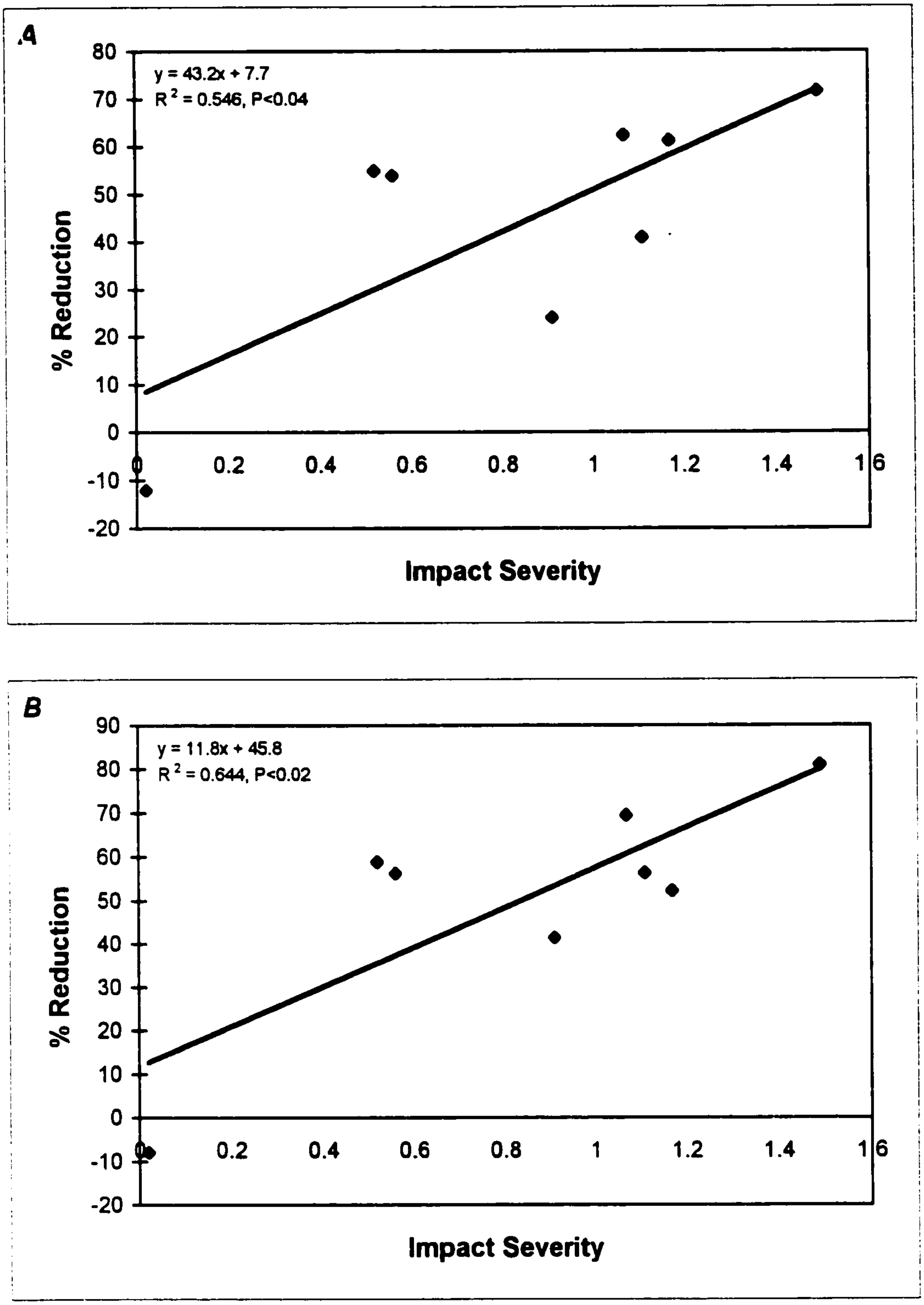


**Figure 3.6. Percent reduction in *Thalassia* biomass (g DW $m^{-2}$) at each site versus the plume discharge impact index for the site between (A) February 1996 - February 1997, and (B) February 1996 - May 1997.**

**Table 3.5.** *Thalassia* leaf productivity (g DW $m^{-2}$ $d^{-1}$) at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | SITES | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 5.87 | 8.19 | 6.52 | 2.67 | 3.99 | 8.06 | 3.47 | 5.28 |
| May-96 | 4.12 | 4.98 | 6.63 | 1.93 | 3.64 | 6.22 | 2.28 | 5.13 |
| Oct-96 | 2.85 | 2.14 | 7.90 | 1.80 | 4.44 | 6.87 | 1.27 | 6.13 |
| Feb-97 | 4.61 (-21.5) | 4.69 (-42.7) | 6.67 (2.3) | 2.01 (-24.7) | 1.30 (-67.4) | 6.16 (-23.6) | 1.94 (-44.1) | 3.56 (-32.6) |
| May-97 | 4.12 (-29.8) | 4.98 (-39.2) | 5.40 (-17.2) | 2.03 (-23.9) | 2.62 (-34.3) | 5.26 (-34.7) | 2.70 (-22.2) | 3.44 (-34.8) |
| Oct-97 | 6.20 (50.5) | 5.21 (4.6) | 4.46 (-17.4) | 2.86 (40.9) | 3.05 (16.4) | 6.30 (19.8) | 2.85 (5.6) | 3.83 (11.3) |

Plots of percent reduction in leaf productivity at each site versus the impact index at the site are shown for the reductions between February 1996 and February 1997, and between February 1996 and May 1997, in Figures 3.7A and 3.7B respectively. Percent reduction in productivity increased with the estimated impact severity index, but the increase between February 1996 and February 1997 fell short of statistical significance (Figures 3.7A,B).

### *Leaf Growth Rate per Shoot*

Values for leaf growth rate per shoot at the 8 sites are shown in Table 3.6. Between February 1996 and February 1997, growth rate decreased at 3 sites and increased at 5. There was no effect of time on growth rate (February-February; Two-Way Analysis of Variance: F=0.45, P=0.84), but a significant effect of site (F=7.21, P<0.001) and a significant interaction between site and time (F=3.90, P<0.001). Between February 1996 and May 1997, growth rate decreased at 5 sites and increased at 3. There was again no effect of time on growth rate (February-May; F=2.72, P=0.14), but a significant effect of site (F=7.37, P<0.001) and a significant interaction between site and time (F=5.73, P<0.001). Between May and October 1997, growth rate increased at 7 sites, and decreased at 1, but the effect of time on growth rate was not significant (F=1.00, P=0.35). However, there was a significant effect of site on growth rate (F=11.90, P<0.001), and a significant interaction between site and time (F=5.58, P<0.001).

### *Plastochron Interval*

Values for plastochron interval at the 8 sites are shown in Table 3.7. Plastochron interval did not change significantly between February 1996 and February 1997 (Paired-Sample t-test: t=0.29, P=0.78), between February 1996 and May 1997 (t=1.12, P=0.30), or between May and October 1997 (t=1.81, P=0.11).

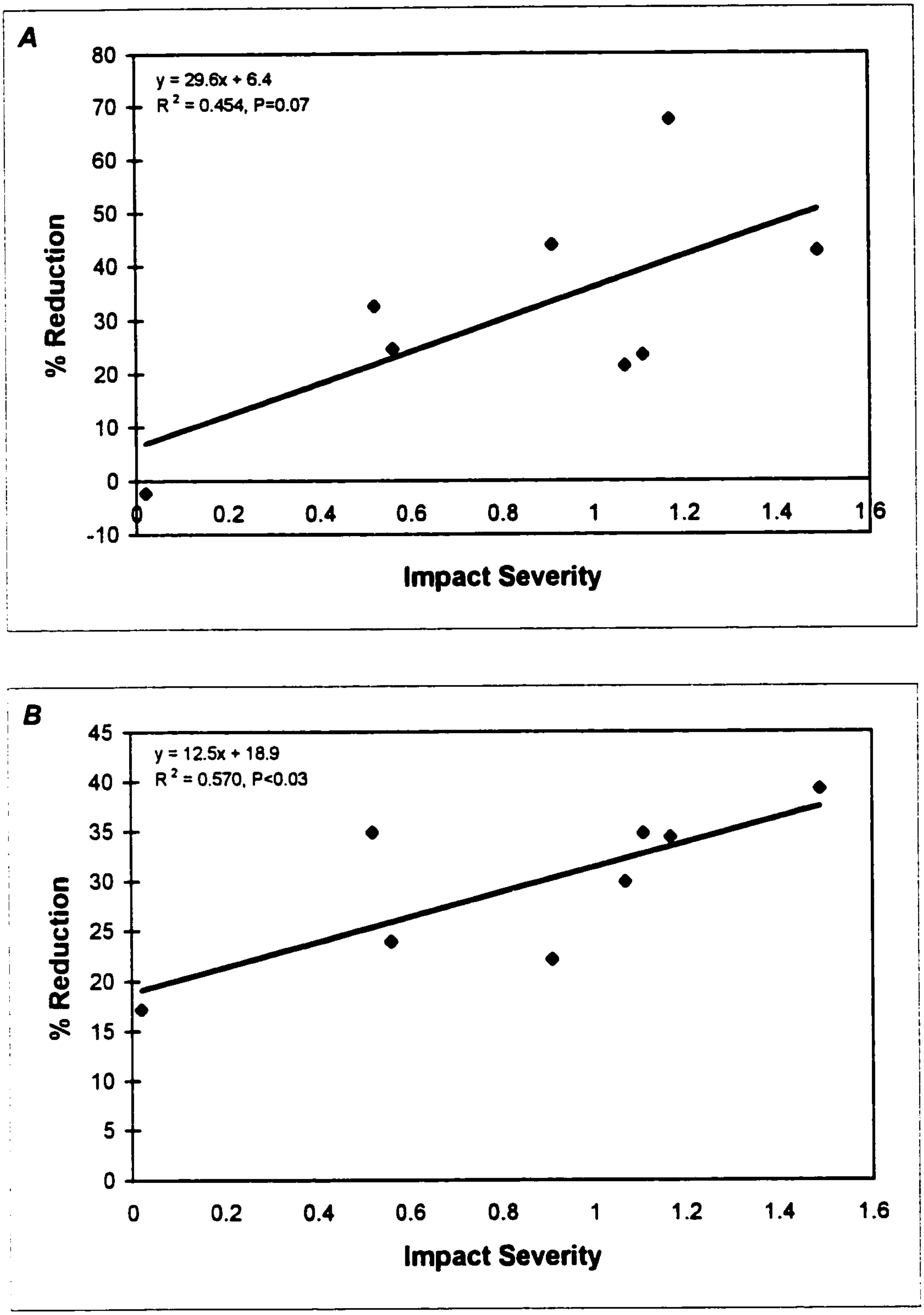


Figure 3.7. Percent reduction in *Thalassia* productivity (g DW $m^{-2}$ $d^{-1}$) at each site versus the plume discharge impact index for the site between (A) February 1996 - February 1997, and (B) February 1996 - May 1997.

**Table 3.6.** *Thalassia* leaf growth rate per shoot (cm $d^{-1}$) at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event. Values are means of 20 shoots for each site ± SE. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | SITES | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 0.47 ± 0.02 | 0.63 ± 0.05 | 0.38 ± 0.02 | 0.41 ± 0.04 | 0.66 ± 0.04 | 0.49 ± 0.03 | 0.57 ± 0.05 | 0.58 ± 0.04 |
| May-96 | 0.57 ± 0.04 | 0.63 ± 0.04 | 0.49 ± 0.02 | 0.51 ± 0.04 | 0.45 ± 0.02 | 0.55 ± 0.05 | 0.53 ± 0.04 | 0.54 ± 0.03 |
| Oct-96 | 0.73 ± 0.05 | 0.38 ± 0.03 | 0.49 ± 0.05 | 0.43 ± 0.05 | 0.51 ± 0.04 | 0.49 ± 0.04 | 0.42 ± 0.04 | 0.61 ± 0.07 |
| Feb-97 | 0.57 ± 0.02<br>(21.3) | 0.55 ± 0.04<br>(-12.7) | 0.46 ± 0.01<br>(21.1) | 0.54 ± 0.03<br>(31.7) | 0.57 ± 0.02<br>(-13.6) | 0.59 ± 0.04<br>(20.4) | 0.48 ± 0.02<br>(-15.8) | 0.59 ± 0.04<br>(1.7) |
| May-97 | 0.36 ± 0.02<br>(-23.4) | 0.36 ± 0.03<br>(-42.9) | 0.40 ± 0.02<br>(5.3) | 0.51 ± 0.04<br>(24.4) | 0.51 ± 0.04<br>(-22.7) | 0.50 ± 0.03<br>(2.0) | 0.41 ± 0.03<br>(-28.1) | 0.57 ± 0.04<br>(-1.7) |
| Oct-97 | 0.69 ± 0.04<br>(91.7) | 0.33 ± 0.02<br>(-8.3) | 0.47 ± 0.02<br>(17.5) | 0.55 ± 0.03<br>(7.8) | 0.56 ± 0.04<br>(9.8) | 0.52 ± 0.04<br>(4.0) | 0.45 ± 0.03<br>(9.8) | 0.61 ± 0.03<br>(7.0) |

**Table 3.7.** *Thalassia* plastochron interval (days) at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | **SITES** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 20 | 12.9 | 17.1 | 26 | 13.5 | 14.3 | 20 | 25 |
| May-96 | 18.9 | 16.7 | 25 | 25 | 14.3 | 22.2 | 25 | 18.2 |
| Oct-96 | 22.8 | 15.2 | 19.5 | 28 | 20 | 28 | 25.1 | 26.7 |
| Feb-97 | 14.4 (-28.0) | 14.7 (14.0) | 22.7 (32.7) | 19 (-26.9) | 20 (48.1) | 14.7 (2.6) | 18 (-10.0) | 21.2 (-15.2) |
| May-97 | 23 (15.0) | 18.9 (46.5) | 23.5 (37.3) | 20.2 (-22.4) | 14.7 (8.7) | 18.2 (26.9) | 15.9 (-20.6) | 28.9 (15.5) |
| Oct-97 | 18 (-21.7) | 22.9 (21.2) | 15.9 (-32.2) | 13.3 (-33.9) | 19 (29.5) | 15 (-17.4) | 13.1 (-17.4) | 20.7 (-28.3) |

### *Relative Leaf Growth Rate per Shoot*

Changes in relative leaf growth rate (cm new tissue • $cm^{-1}$ old tissue • $d^{-1}$) at the 8 sites are shown in Table 3.8. Between February 1996 and February 1997, relative leaf growth rate increased at 5 sites. There was a weak effect of time (February-February; Two-Way Analysis of Variance: F=4.49, P=0.07), and a significant effect of site (F=7.41, P<0.001) on relative leaf growth rate. The interaction between site and time was significant (F=6.74, P<0.001). Between February 1996 and May 1997, relative leaf growth rate increased at all 8 sites. There was a significant effect of time (February-May: F=26.5, P<0.001) and site (F=4.81, P<0.001) on relative leaf growth rate, and a significant interaction between site and time (F=6.02, P<0.001). Between May and October 1997, relative leaf growth rate decreased at 6 sites and increased at 2. There was a significant effect of time (May-October: F=8.02, P<0.03) and site (F=8.09, P<0.001) on relative leaf growth rate, and a significant interaction effect between site and time (F=3.84, P<0.001).

The percent reduction in relative leaf growth rate at each site between February 1996 and February 1997, and between February 1996 and May 1997, was not correlated with the impact indices at the sites (Figures 3.8A,B).

### *Specific Leaf Productivity Rate*

Changes in specific leaf productivity rate (mg $g^{-1}$ $d^{-1}$) at the 8 sites are shown in Table 3.9. Specific leaf productivity rate increased at 5 of the 8 sites between February 1996 and February 1997, and increased at all 8 sites between February 1996 and May 1997. For all sites combined, specific leaf productivity rate was significantly higher in February 1997 than Febrary 1996 (Paired sample t-test, paired by site: t=2.41, P<0.05), and significantly higher in May 1997 than February 1996 (t=3.73, P<0.01). Specific leaf productivity rate decreased at 6 of the 8 sites between May and October 1997 (i.e. after discharge; Table 3.9); for all sites

**Table 3.8.** *Thalassia* relative leaf growth rate (cm new tissue • cm$^{-1}$ old tissue • d$^{-1}$) at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event. Values are means of 20 shoots for each site ± SE. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | SITES | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 0.035±0.003 | 0.043±0.005 | 0.059±0.003 | 0.029±0.003 | 0.056±0.002 | 0.040±0.002 | 0.059±0.011 | 0.036±0.004 |
| May-96 | 0.064±0.005 | 0.059±0.009 | 0.047±0.002 | 0.066±0.006 | 0.048±0.005 | 0.064±0.003 | 0.068±0.007 | 0.043± 0.003 |
| Oct-96 | 0.141±0.03 | 0.043±0.007 | 0.051±0.003 | 0.073±0.03 | 0.069±0.005 | 0.062±0.01 | 0.059±0.008 | 0.064± 0.006 |
| Feb-97 | 0.060±0.008<br>(71.4) | 0.083±0.009<br>(93.0) | 0.052±0.004<br>(-11.9) | 0.056±0.005<br>(93.1) | 0.064±0.006<br>(14.3) | 0.035±0.002<br>(-12.5) | 0.054±0.004<br>(-8.5) | 0.069±0.007<br>(91.7) |
| May-97 | 0.110±0.009<br>(214.3) | 0.095±0.005<br>(120.9) | 0.065±0.004<br>(10.2) | 0.073±0.01<br>(151.7) | 0.082±0.005<br>(46.4) | 0.071±0.005<br>(77.5) | 0.086±0.003<br>(45.8) | 0.067±0.006<br>(86.1) |
| Oct-97 | 0.097±0.012<br>(-11.8) | 0.048±0.005<br>(-49.5) | 0.072±0.011<br>(10.8) | 0.075±0.009<br>(2.7) | 0.050±0.005<br>(-39.0) | 0.055±0.007<br>(-22.5) | 0.077±0.007<br>(-10.5) | 0.061±0.004<br>(-9.8) |

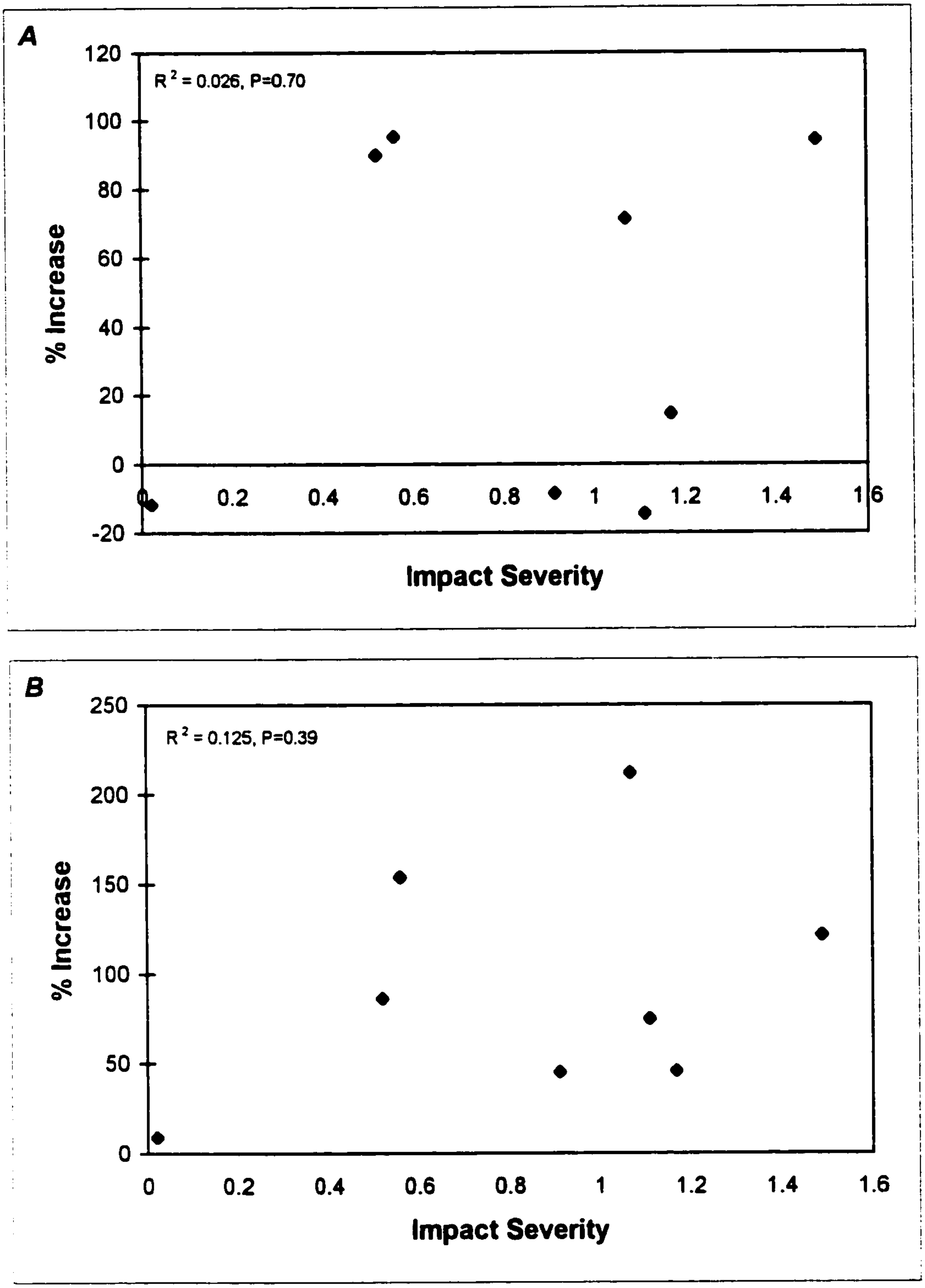


Figure 3.8. Linear regression of percent increase in *Thalassia* relative leaf growth rate (cm $cm^{-1}$ $d^{-1}$) at each site versus the plume discharge impact index between (A) February 1996 - February 1997, and (B) February 1996 - May 1997.

**Table 3.9.** *Thalassia* specific leaf productivity rate (mg $g^{-1}$ $d^{-1}$) at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | SITES | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 17.75 | 20.63 | 23.71 | 24.50 | 19.0 | 24.13 | 16.84 | 19.63 |
| May-96 | 11.38 | 19.01 | 27.97 | 22.98 | 18.02 | 25.39 | 14.16 | 21.11 |
| Oct-96 | 12.56 | 15.97 | 47.31 | 27.27 | 52.24 | 40.89 | 11.55 | 43.79 |
| Feb-97 | 30.73<br>(108.4) | 41.50<br>(101.2) | 21.66<br>(-8.7) | 40.2<br>(64.1) | 15.85<br>(-16.6) | 31.27<br>(29.6) | 15.77<br>(-6.4) | 29.42<br>(49.9) |
| May-97 | 33.77<br>(129.0) | 66.40<br>(221.9) | 31.40<br>(32.4) | 42.29<br>(72.7) | 26.20<br>(37.9) | 36.28<br>(50.3) | 27.84<br>(65.2) | 31.27<br>(59.3) |
| Oct-97 | 31.96<br>(-5.4) | 45.70<br>(-31.2) | 28.23<br>(10.1) | 31.78<br>(-24.9) | 37.65<br>(43.7) | 24.23<br>(-33.2) | 24.57<br>(-11.7) | 23.21<br>(-25.8) |

combined, the decrease was not statistically significant (t=1.81, P=0.11).

Plots of percent increase in specific leaf productivity rate at each site vs the impact index at the site are shown for the increases between February 1996 and February 1997, and between February 1996 and May 1997 (Figures 3.9A,B). Percent increase in specific leaf productivity rate was not significantly correlated with the impact index in either case (Figures 3.9A,B).

### *Leaves per Shoot*

Values for leaves per shoot at the 8 sites are shown in Table 3.10. Between February 1996 and February 1997, leaves per shoot decreased at 5 sites, remained unchanged at 1, and increased marginally at 2 sites. There was a significant effect of time (Two-Way Analysis of Variance: F=10.60, P<0.01) and site (F=8.905, P<0.001) on leaves per shoot, and a significant interaction between site and time (F=2.634, P<0.01). Between February 1996 and May 1997, leaves per shoot decreased at 4 sites, remained unchanged at 1, and increased at 3 sites. There was a significant effect of site (F=4.44, P<0.001), but not of time (F=1.36, P=0.28) on leaf density. The interaction effect between site and time was significant (F=3.87, P<0.001). Between May and October 1997, leaves per shoot increased at 5 sites, remained unchanged at 1, and decreased at 2 sites. There was a significant effect of site (F=3.27, P<0.002), but not of time (F=1.24, P=0.30) on leaves per shoot. The interaction effect between site and time was significant (F=4.56, P<0.001).

The percent reduction in leaves per shoot at each site between February 1996 and February 1997 was not correlated with the impact indices at the sites (Figure 3.10).

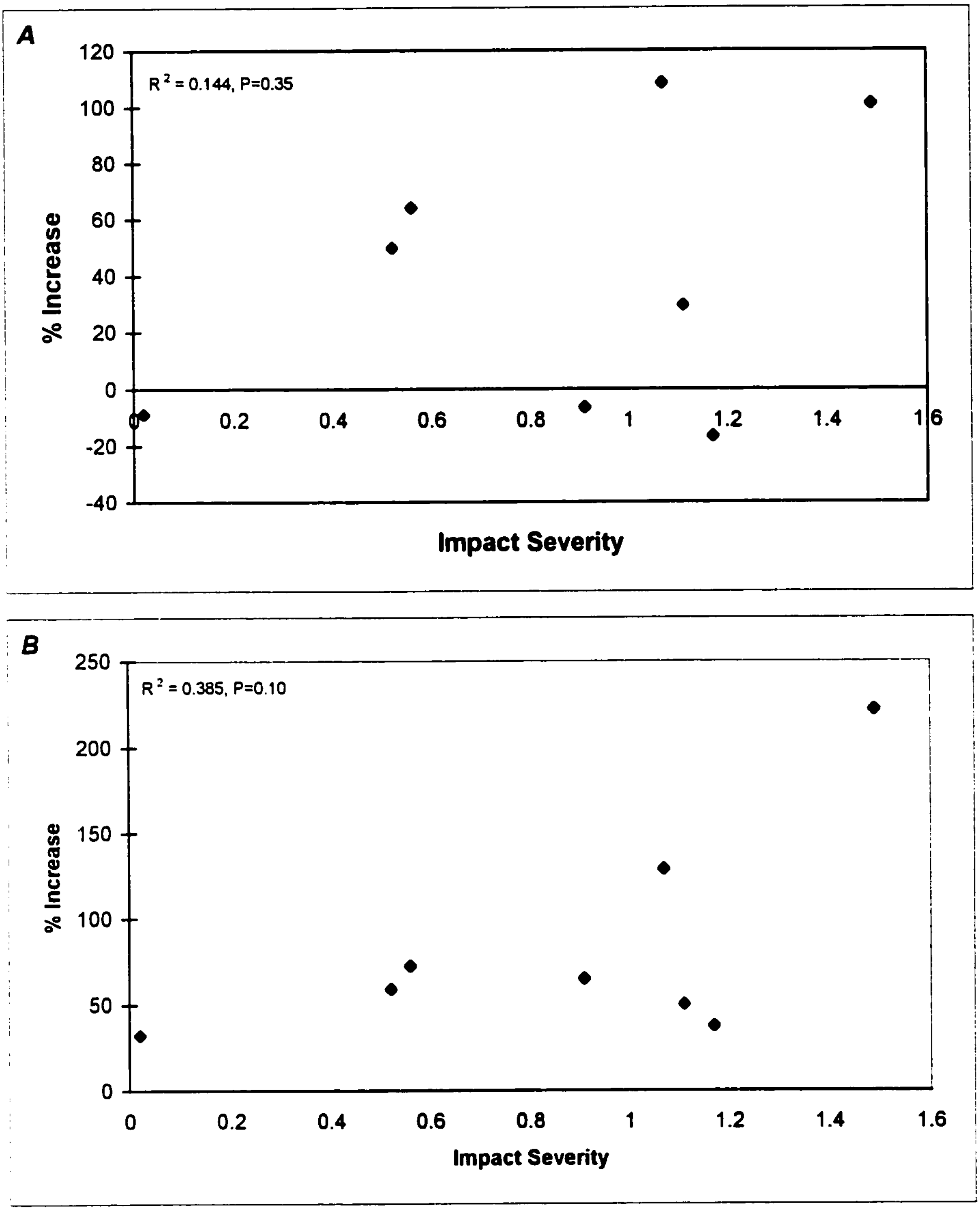


**Figure 3.9. Linear regression of percent increase in *Thalassia* specific leaf productivity rate (mg $g^{-1}$ $d^{-1}$) at each site versus the plume discharge impact index between (A) February 1996 - February 1997, and (B) February 1996 - May 1997.**

**Table 3.10.** *Thalassia* leaves per shoot at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event. Values are means of 20 shoots for each site ± SE. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | SITES | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 3.0 ± 0.11 | 3.2 ± 0.11 | 2.7 ± 0.11 | 3.3 ± 0.10 | 3.4 ± 0.17 | 3.2 ± 0.16 | 3.0 ± 0.13 | 3.2 ± 0.14 |
| May-96 | 3.1 ± 0.15 | 3.1 ± 0.10 | 2.7 ± 0.07 | 3.0 ± 0.13 | 3.0 ± 0.17 | 3.1 ± 0.17 | 3.0 ± 0.11 | 3.6 ± 0.11 |
| Oct-96 | 2.3 ± 0.13 | 2.0 ± 0.06 | 3.1 ± 0.10 | 3.1 ± 0.23 | 2.6 ± 0.11 | 3.1 ± 0.13 | 2.3 ± 0.09 | 3.1 ± 0.15 |
| Feb-97 | 2.6 ± 0.18<br>(-13.3) | 2.8 ± 0.12<br>(-12.5) | 2.8 ± 0.13<br>(3.7) | 2.4 ± 0.14<br>(-27.3) | 3.4 ± 0.18<br>(0) | 3.3 ± 0.16<br>(3.1) | 2.5 ± 0.08<br>(-16.7) | 2.9 ± 0.11<br>(-9.4) |
| May-97 | 3.3 ± 0.14<br>(9.1) | 2.4 ± 0.15<br>(-33.3) | 2.8 ± 0.09<br>(3.6) | 3.1 ± 0.25<br>(-6.5) | 3.4 ± 0.15<br>(0) | 2.7 ± 0.13<br>(-18.5) | 3.2 ± 0.19<br>(6.3) | 2.7 ± 0.13<br>(-18.5) |
| Oct-97 | 3.6 ± 0.17<br>(9.1) | 3.0 ± 0.13<br>(25.0) | 3.2 ± 0.14<br>(14.3) | 3.1 ± 0.19<br>(0) | 2.7 ± 0.20<br>(-20.6) | 3.3 ± 0.13<br>(22.2) | 3.0 ± 0.14<br>(-6.3) | 3.2 ± 0.11<br>(18.5) |

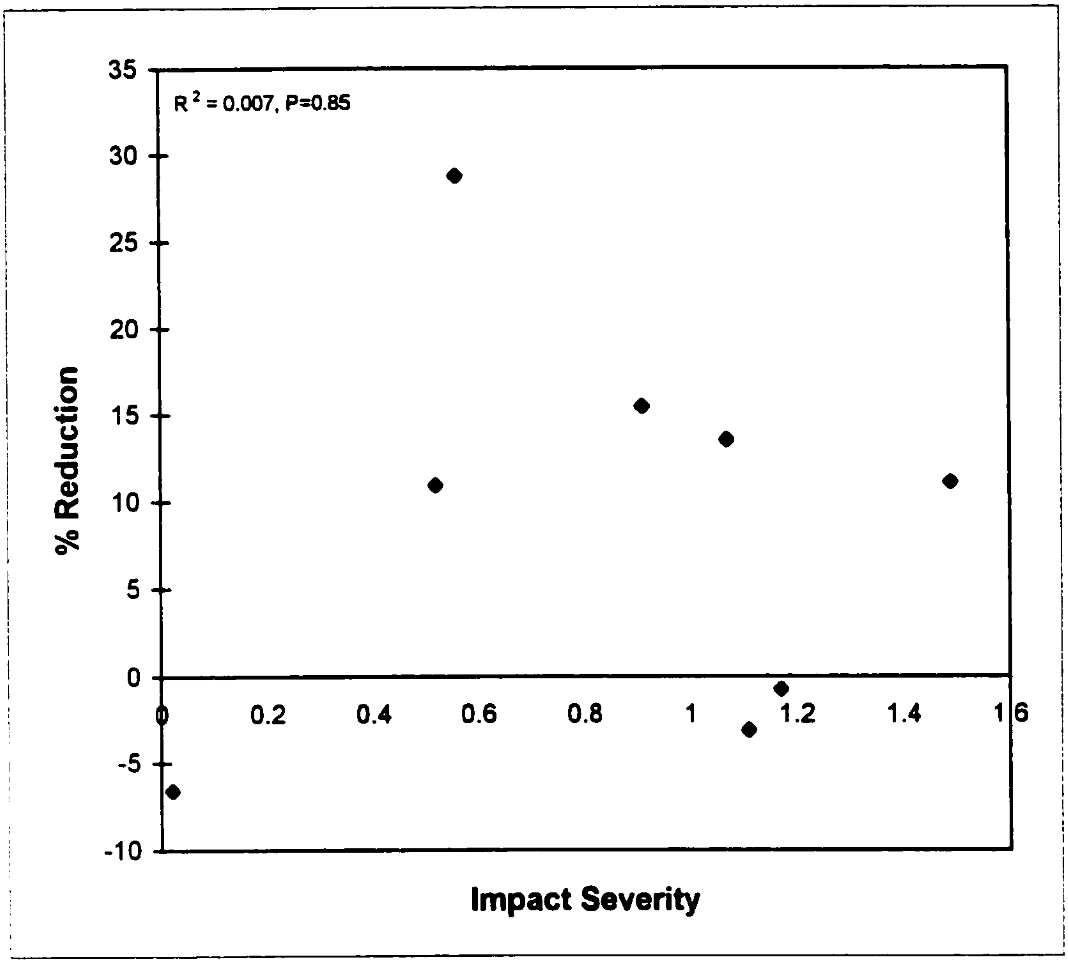


Figure 3.10. Percent reduction in *Thalassia* leaves per shoot at each site versus the plume discharge impact index for the site between February 1996 and February 1997.

### *Width*

Changes in leaf width (cm) at the 8 sites are shown in Table 3.11. Between February 1996 and February 1997, leaf width decreased at 7 sites. There was a significant effect of time (Two-Way Analysis of Variance: F=14.07, P<0.007), and site (F=2.28, P<0.03) on leaf width, and a significant interaction between site and time (F=7.12, P<0.001). Between February 1996 and May 1997, leaf width decreased at 7 sites and remained unchaged at 1. There was a significant effect of time (F=6.78, P<0.04), and site (F=18.48, P<0.001) on leaf width, and a significant interaction between site and time (F=19.18, P<0.001). Between May and October 1997, leaf width increased at 5 sites, decreased at 2 and was unchanged at 1. There was no effect of time on leaf width (F=0.66, P=0.45), but a significant effect of site (F=14.84, P<0.001) and a significant interaction between site and time (F=13.18, P<0.001).

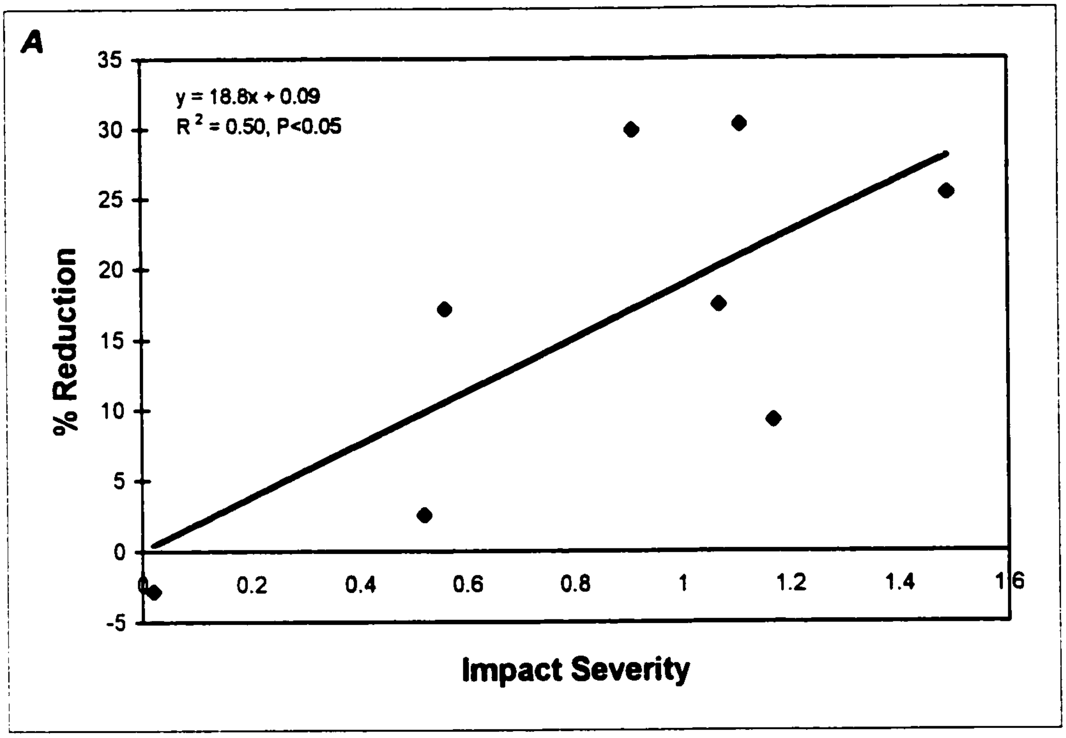
The percent reduction in leaf width at each site between February 1996 and February 1997, and between February 1996 and May 1997, was significantly correlated with the impact indices at the sites (Figures 3.11A,B).

### *Length*

Values for maximum leaf length (cm) at the 8 sites are shown in Table 3.12. Between February 1996 and February 1997, leaf length decreased at 6 sites but the effect of time on leaf length was not significant (Two-Way Analysis of Variance: F=3.34, P=0.11). There was a significant effect of site on leaf length (F=11.95, P<0.001), and a significant interaction between site and time (F=20.3, P<0.001). Between February 1996 and May 1997, leaf length also decreased at 6 sites, but the effect of time on leaf length was again not significant (F=1.45, P=0.27). There was a significant effect of site on leaf length (F=15.06, P<0.001), and a significant interaction between site and time (F=36.68, P<0.001). Between May and October 1997, leaf length increased at 5 sites. There was no effect of time on leaf length

**Table 3.11.** *Thalassia* leaf width (cm) at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event. Values are means of 20 shoots for each site ± SE. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | **SITES** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 1.06 ± 0.03 | 1.14 ± 0.04 | 1.06 ± 0.04 | 1.16 ± 0.02 | 1.07 ± 0.02 | 1.27 ± 0.03 | 1.15 ± 0.02 | 1.07 ± 0.02 |
| May-96 | 0.93 ± 0.15 | 1.27 ± 0.03 | 1.10 ± 0.02 | 1.15 ± 0.07 | 1.15 ± 0.04 | 1.26 ± 0.03 | 1.09 ± 0.04 | 1.23 ± 0.04 |
| Oct-96 | 0.72 ± 0.02 | 1.13 ± 0.02 | 1.16 ± 0.02 | 1.19 ± 0.04 | 1.09 ± 0.04 | 1.04 ± 0.03 | 0.86 ± 0.01 | 1.23 ± 0.04 |
| Feb-97 | 0.88 ± 0.04<br>(-17.0) | 0.85 ± 0.04<br>(-25.4) | 1.09 ± 0.07<br>(2.8) | 0.96 ± 0.03<br>(-17.2) | 0.97 ± 0.02<br>(-9.3) | 0.89 ± 0.06<br>(-29.9) | 0.81 ± 0.01<br>(-29.6) | 1.05 ± 0.04<br>(-1.9) |
| May-97 | 1.03 ± 0.04<br>(-2.8) | 0.64 ± 0.02<br>(-43.9) | 1.06 ± 0.02<br>(0) | 1.04 ± 0.03<br>(-10.3) | 0.93 ± 0.03<br>(-13.1) | 1.08 ± 0.03<br>(-15.0) | 0.87 ± 0.03<br>(-24.3) | 1.03 ± 0.04<br>(-3.7) |
| Oct-97 | 1.03 ± 0.03<br>(0) | 1.03 ± 0.04<br>(60.9) | 0.95 ± 0.04<br>(10.4) | 1.08 ± 0.05<br>(3.8) | 1.02 ± 0.04<br>(9.7) | 0.95 ± 0.03<br>(-12.0) | 0.86 ± 0.03<br>(-1.1) | 1.15 ± 0.03<br>(11.7) |



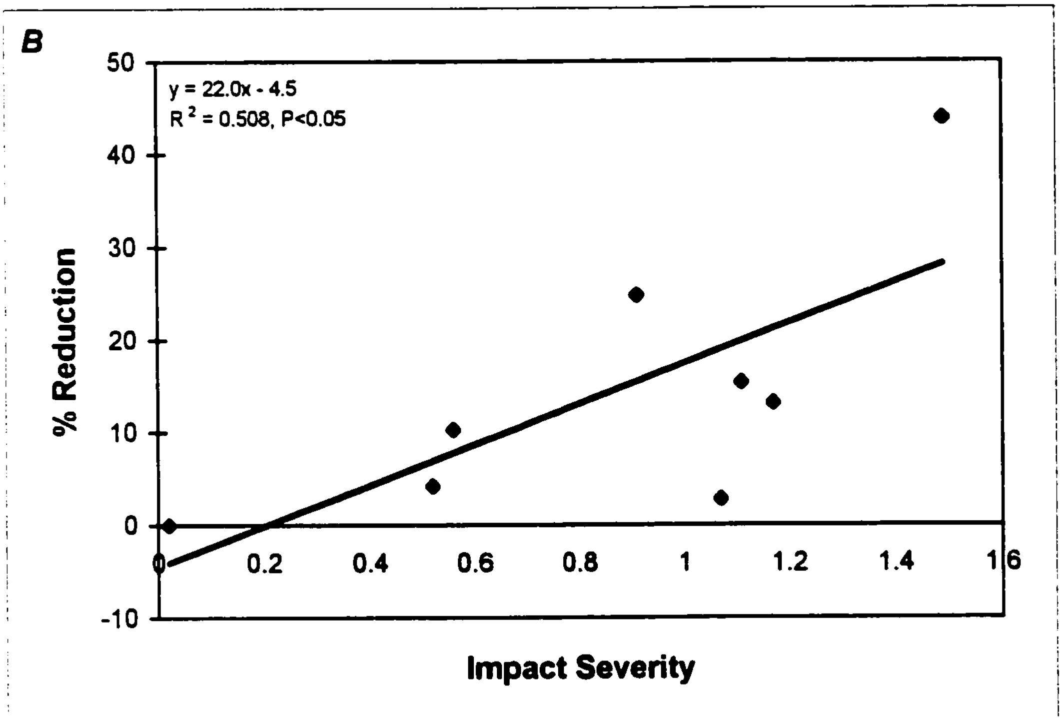


**Figure 3.11. Percent reduction in *Thalassia* leaf width (cm) at each site versus the plume discharge impact index for the site between (A) February 1996 - February 1997, and (B) February 1996 - May 1997.**

**Table 3.12.** *Thalassia* leaf length (cm) at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event. Values are means of 20 shoots for each site ± SE. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | SITES | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 19.46±0.90 | 27.09±0.85 | 21.28±0.59 | 22.69±0.63 | 18.94±0.68 | 20.59±0.72 | 22.05±0.74 | 27.01±1.08 |
| May-96 | 22.04±0.98 | 25.49±0.92 | 19.42±0.59 | 17.02± 1.23 | 19.51±0.96 | 18.00±0.72 | 16.42±0.46 | 22.98±0.87 |
| Oct-96 | 16.87±1.02 | 18.46±0.77 | 20.53±0.63 | 17.76± 1.33 | 14.85±0.80 | 18.65±0.99 | 12.55±0.43 | 21.97±1.16 |
| Feb-97 | 16.55±0.52<br>(-15.0) | 15.70±0.29<br>(-42.0) | 17.45±0.76<br>(-18.0) | 20.84± 1.05<br>(-8.2) | 23.36±0.72<br>(22.8) | 23.04±1.44<br>(27.7) | 14.89±0.63<br>(-32.5) | 20.72±0.63<br>(-23.3) |
| May-97 | 16.58±0.67<br>(-14.8) | 10.65±0.59<br>(-60.7) | 16.60±0.67<br>(-22.0) | 20.97±1.54<br>(-7.6) | 22.34±0.92<br>(18.0) | 29.01±0.98<br>(40.9) | 18.32±0.83<br>(-16.9) | 19.68±0.84<br>(-27.1) |
| Oct-97 | 19.58±0.65<br>(18.9) | 17.52±0.67<br>(64.5) | 21.08±0.81<br>(27.0) | 21.38±1.52<br>(2.0) | 20.91±1.26<br>(-6.4) | 22.42±1.25<br>(-22.7) | 14.71±0.78<br>(-19.7) | 23.28±0.82<br>(18.3) |

(F=0.28, P=0.61), but a significant effect of site (F=27.31, P<0.001) and a significant interaction between site and time (F=10.76, P<0.001).

### 3.4.2.3 *Changes in Syringodium Abundance*

Changes in *Syringodium* shoot density (shoots m$^{-2}$) at the 8 sites before, during and after the discharge event are shown in Table 3.13. *Syringodium* did not occur at sites 1 and 2. Shoot densities increased at 4 of the remaining 6 sites between February 1996 and February 1997, and increased at 5 of the 6 sites between February 1996 and May 1997. For the 6 sites combined, shoot densities did not differ significantly between February 1996 and February 1997 (Paired-Sample t-test, paired by site: t=0.68, P=0.52), nor between February 1996 and May 1997 (t=1.03, P=0.35). Shoot densities increased at 5 sites between May and October 1997, but the increase was not statistically significant (t=1.96, P=0.11).

### 3.4.2.4 *Changes in Water Quality*

Values for chlorophyll-*a*, nitrates, phosphates, SPM, salinity and turbidity at the plume discharge point and at 6 of the 8 sites before and during discharge are shown in Table 3.14. There was no effect of time on chlorophyll-*a* concentrations (before discharge - during discharge; Two-Way Analysis of Variance: F=1.20, P=0.32), but a significant effect of site (F=349.79, P<0.001) and a significant interaction between site and time (F=335.15, P<0.001). There was no effect of time on phosphate concentrations (F=0.43, P=0.54), but a significant effect of site (F=16.82, P<0.001), and a significant interaction between site and time (F=9.90, P<0.001). There was no effect of time on salinity (F=2.48, P=0.17), but a significant effect of site (F=22.09, P<0.001), and a significant interaction between site and time (F=16.24, P<0.001).

**Table 3.13.** *Syringodium* shoot density (shoots m$^{-2}$) at 6 of the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event. Percent changes (in parentheses) between February 1996 and February 1997 (1 year after discharge), between February 1996 and May 1997 (full discharge period) and between May 1997 and October 1997 (post-discharge period) are shown.

| | | | SITE | | | |
|---|---|---|---|---|---|---|
| **Months** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 2528 | 5120 | 7488 | 1600 | 4896 | 4480 |
| May-96 | 2584 | 4880 | 7680 | 1536 | 5424 | 4344 |
| Oct-96 | 3128 | 5760 | 6848 | 2224 | 5256 | 4792 |
| Feb-97 | 2348 (-7.1) | 6760 (32.0) | 6368 (-15.0) | 1984 (24.0) | 5028 (2.7) | 5160 (15.2) |
| May-97 | 2680 (6.0) | 7376 (44.1) | 5360 (-28.4) | 3640 (127.5) | 5608 (14.5) | 5460 (21.9) |
| Oct-97 | 2976 (11.0) | 8320 (12.8) | 6720 (25.4) | 4560 (25.3) | 6232 (11.1) | 4760 (-12.8) |

**Table 3.14.** Water quality variables before (*A*) and during (*B*) discharge. Site 0 is at point of discharge. Locations of other sites as shown in Figure 3.1. Chlorophyll-*a* (chl-*a*) in mg m$^{-3}$, nitrates ($NO_3$-N) and phosphates ($PO_4$-P) in $\mu$g-at l$^{-1}$, suspended particulate matter (SPM) in mg l$^{-1}$, salinity in ppm, and turbidity in nephelometer turbidity units (NTU). Values are means of 5 samples ± SE. Percent changes for variables which differed significantly before and during discharge are shown in parentheses.

| **SITE** | | **WATER QUALITY VARIABLE** | | | | | |
|---|---|---|---|---|---|---|---|
| | | **Chl-*a*** | **$NO_3$-N** | **$PO_4$-P** | **SPM** | **Salinity** | **Turbidity** |
| **0** | ***A*** | 0.40 ± 0.02 | 0.96 ± 0.002 | 0.05 ± 0.01 | 4.86 ± 2.02 | 34.4 ± 0.24 | 1.2 ± 0.01 |
| | ***B*** | 3.34 ± 0.07 | 7.55 ± 0.93 | 0.12 ± 0.01 | 31.74 ± 2.60 | 26.8 ± 1.18 | 112.0 ± 5.2 |
| **1** | ***A*** | 0.32 ± 0.01 | 0.80 ± 0.13 | 0.03 ± 0.002 | 6.10 ± 1.78 | 35.2 ± 0.20 | 1.2 ± 0.01 |
| | ***B*** | 0.35 ± 0.02 | 1.08 ± 0.03 (35.0) | 0.03 ± 0.01 | 9.80 ± 0.58 (60.7) | 34.6 ± 0.24 | 53.4 ± 1.9 (4389) |
| **2** | ***A*** | 0.29 ± 0.01 | 0.96 ± 0.04 | 0.03 ± 0.002 | 4.88 ± 1.08 | 34.8 ± 0.20 | 1.20 ± 0.005 |
| | ***B*** | 0.79 ± 0.03 | 2.42 ± 0.06 (152.1) | 0.04 ± 0.01 | 12.12 ± 0.02 (148.4) | 33.2 ± 0.43 | 62.76 ± 1.50 (5130) |
| **3** | ***A*** | 0.32 ± 0.01 | 0.74 ± 0.04 | 0.03 ± 0.002 | 4.26 ± 0.83 | 35.0 ± 0.001 | 1.01 ± 0.007 |
| | ***B*** | 0.25 ± 0.004 | 0.82 ± 0.01 (10.8) | 0.02 ± 0.01 | 4.65 ± 0.18 (9.2) | 34.6 ± 0.43 | 27.82 ± 0.94 (2654) |
| **5** | ***A*** | 0.39 ± 0.01 | 0.86 ± 0.18 | 0.04 ± 0.01 | 7.05 ± 1.32 | 35.0 ± 0.32 | 1.18 ± 0.009 |
| | ***B*** | 0.28 ± 0.04 | 1.20 ± 0.12 (39.5) | 0.01 ± 0.01 | 10.60 ± 0.43 (50.4) | 34.6 ± 0.99 | 66.44 ± 1.56 (5531) |
| **6** | ***A*** | 0.40 ± 0.01 | 0.48 ± 0.003 | 0.04 ± 0.01 | 4.58 ± 0.96 | 34.6 ± 0.24 | 1.15 ± 0.008 |
| | ***B*** | 0.31 ± 0.08 | 0.90 ± 0.09 (87.5) | 0.02 ± 0.01 | 10.75 ± 0.46 (134.7) | 34.6 ± 0.45 | 74.6 ± 1.63 (6387) |
| **8** | ***A*** | 0.38 ± 0.01 | 0.88 ± 0.08 | 0.02 ± 0.001 | 5.58 ± 2.35 | 35.2 ± 0.20 | 1.02 ± 0.008 |
| | ***B*** | 0.29 ± 0.03 | 1.11 ± 0.01 (26.1) | 0.03 ± 0.01 | 8.10 ± 0.43 (45.2) | 34.6 ± 0.45 | 56.12 ± 2.20 (5402) |

There was a significant effect of time on nitrate concentrations, with values being higher during discharge than before discharge (Table 3.14; F=7.09, P<0.04). There was a signficant effect of site on nitrate concentration (F=47.62, P<0.001), and a significant interaction between site and time (F=22.98, P<0.001). Percent changes in nitrate concentrations before and during discharge at the 6 study sites were weakly correlated with the impact indices at the sites (Figure 3.12A).

There was a significant effect of time on SPM values, with values being higher during discharge than before discharge (Table 3.13; F=6.09, P<0.05). There was no effect of site on SPM values (F=0.69, P=0.65), but a significant interaction between site and time (F=3.94, P<0.002). Percent changes in SPM values before and during discharge at the 6 sites were significantly correlated with the impact indices at the sites (Figure 3.12B).

There was a significant effect of time on turbidity, with values being higher during discharge than before discharge (F=43.72, P<0.001). There was a significant effect of site on turbidity level (F=105.80, P<0.001), and a significant interaction between site and time (F=104.89, P<0.001). The relationship between percent changes in turbidity values and the impact indices at the sites was positive, but not statistically significant at the small sample size (Figure 3.12C).

#### 3.4.2.5 *Changes in Sedimentation*

Sedimentation rates and sediment organic content at the 8 sites during and after discharge are shown in Table 3.15. There was a significant effect of time on sedimentation rates, the rates being higher during discharge than after discharge (Two-Way Analysis of Variance: F=8.96, P<0.02). There was a significant effect of site on sedimentation rates (F=19.45, P<0.001), and a significant interaction between site and time (F=0.87, P=0.53). The percent decreases in sedimenation rates at the sites following cessation of discharge were

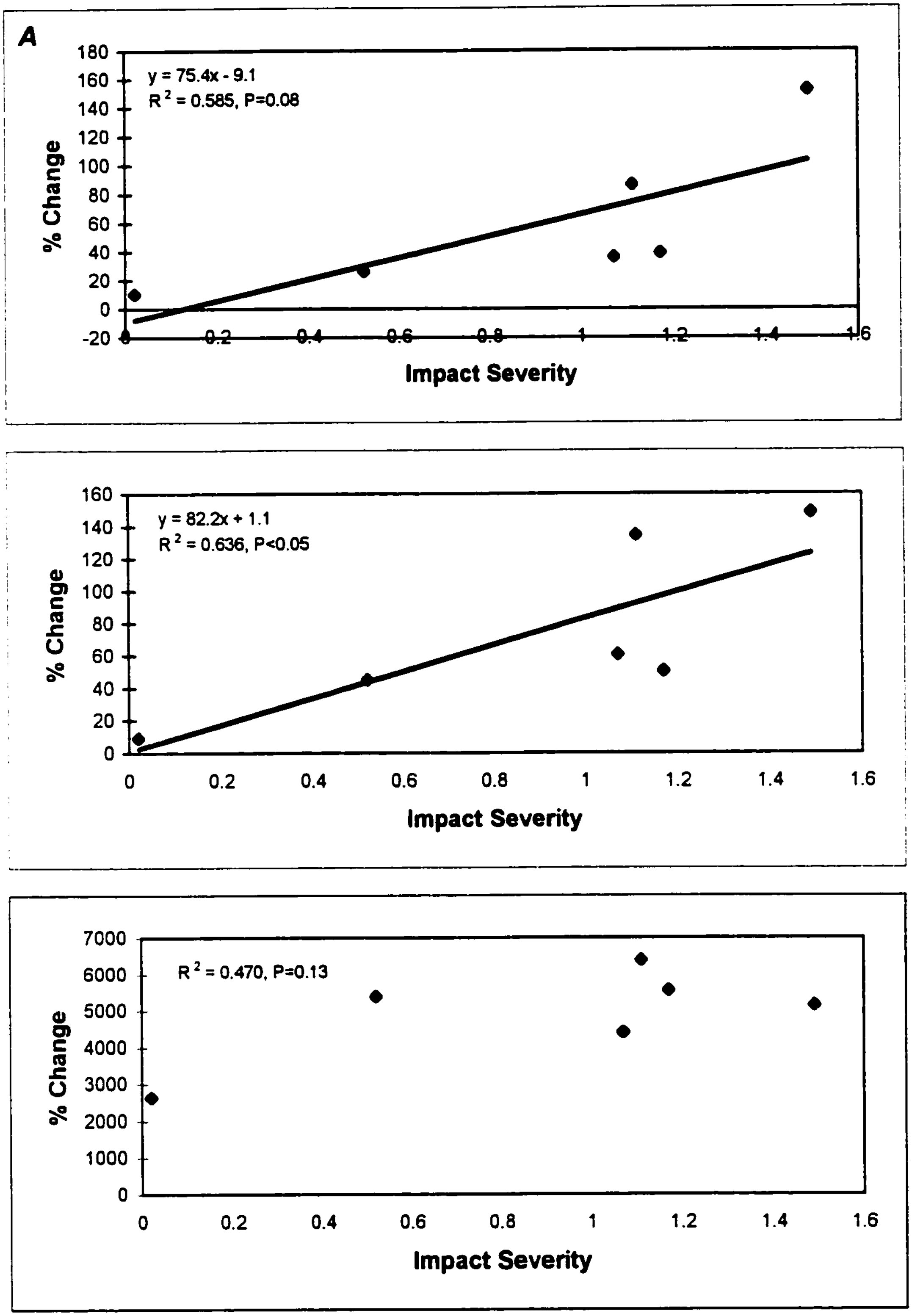


**Figure 3.12. Percent changes in (A) Nitrates, (B) SPM and (C) Turbidity before and during discharge at each site versus the plume discharge impact index for the site.**

**Table 3.15.** Organic content (% AFDW of DW) and sedimentation rate (g DW sediment $m^{-2}$ $d^{-1}$) (A) during discharge and (B) following cessation of discharge. Values are means of 10 samples during discharge and 7 samples following discharge. Standard errors are shown. Percent changes are shown in parentheses.

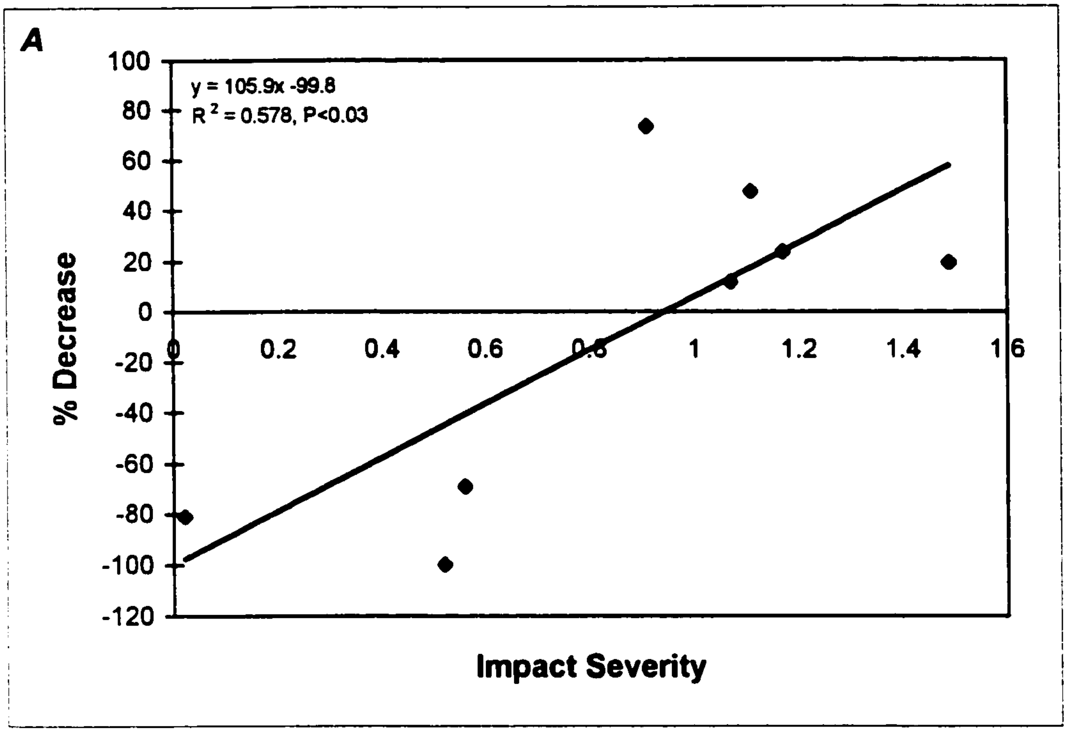
| SITE | | SEDIMENT VARIABLE | |
|---|---|---|---|
| | | **Organic Content** | **Sedimentation Rate** |
| 1 | *A* | 2.44 ± 0.22 | 1.49 ± 0.25 |
| | *B* | 1.68 ± 0.14 (-31.1) | 1.31 ± 0.23 (-12.1) |
| 2 | *A* | 2.78 ± 0.31 | 1.25 ± 0.17 |
| | *B* | 2.32 ± 0.35 (-16.5) | 1.01 ± 0.28 (-19.2) |
| 3 | *A* | 2.87 ± 0.34 | 0.54 ± 0.07 |
| | *B* | 2.32 ± 0.41 (-19.2) | 0.98 ± 0.18 (81.5) |
| 4 | *A* | 5.40 ± 0.63 | 0.04 ± 0.01 |
| | *B* | 2.30 ± 3.35 (-57.4) | 0.07 ± 0.01 (75.0) |
| 5 | *A* | 2.21 ± 0.31 | 1.12 ± 0.10 |
| | *B* | 2.48 ± 0.14 (-12.2) | 0.85 ± 0.19 (-24.1) |
| 6 | *A* | 3.16 ± 0.49 | 0.88 ± 0.14 |
| | *B* | 2.99 ± 0.34 (-5.4) | 0.46 ± 0.12 (-47.7) |
| 7 | *A* | 4.57 ± 0.28 | 0.46 ± 0.16 |
| | *B* | 2.14 ± 2.45 (-53.2) | 0.12 ± 0.03 (-73.9) |
| 8 | *A* | 3.99 ± 0.41 | 0.12 ± 0.20 |
| | *B* | 2.93 ± 0.73 (-26.6) | 0.23 ± 0.13 (91.7) |

signficantly correlated with the impact indices at the sites (Figure 3.13A).

There was a significant effect of time on sediment organic content, with organic content being higher during than after discharge (F=6.09, P<0.04). There was no effect of site on organic content (F=0.93, P=0.48), and no interaction between site and time (F=0.53, P=0.81). The percent decreases in organic content at the sites following cessation of discharge were not significantly correlated with the impact indices at the sites (Figure 3.13B).

### 3.4.2.6 *Changes in Epiphyte Abundance*

Biomass of fleshy epiphytes on *Thalassia* leaves at the 8 sites before, during and after the discharge event are shown in Table 3.16. Biomass of fleshy epiphytes showed substantial temporal and spatial variation (Table 3.16). Epiphyte biomass did not change significantly between February 1996 and February 1997 (Paired-Sample t-test: t=0.52, P=0.62), between February 1996 and May 1997(t=1.67, P=0.14), or between May and October 1997 (t=1.22, P=0.26), indicating no consistent effect of the discharge event on epiphyte levels.



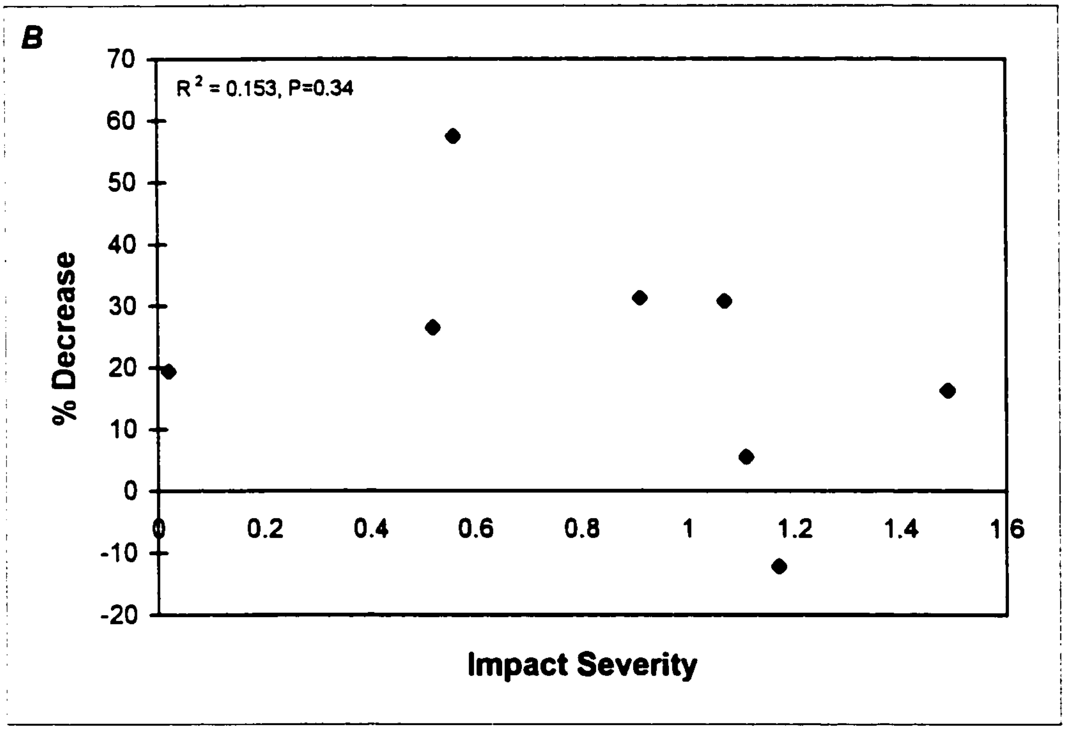


Figure 3.13. Percent decreases in (A) sedimentation rates and (B) % sediment organic content during and after discharge at each site versus the plume discharge impact index for the site.

**Table 3.16.** Fleshy epiphyte biomass (as percent biomass of *Thalassia* leaf biomass) at the 8 sites in St. Lawrence Bay before (February 1996), during (May 1996-May 1997) and after (October 1997) the discharge event.

| | | | | | SITES | | | |
|---|---|---|---|---|---|---|---|---|
| **Months** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Feb-96 | 23.07 | 1.44 | 2.25 | 24.52 | 2 | 0 | 0 | 0 |
| May-96 | 17.55 | 0.52 | 1.64 | 0 | 0 | 0 | 0 | 0 |
| Oct-96 | 1.01 | 0.17 | 0 | 0 | 0 | 0 | 0 | 0 |
| Feb-97 | 7.58 | 5.18 | 20.78 | 0 | 0 | 0.95 | 0 | 0 |
| May-97 | 6.75 | 0.54 | 0 | 0 | 0 | 1.26 | 0 | 0 |
| Oct-97 | 5.64 | 6.30 | 0.28 | 0 | 0 | 3.98 | 0 | 0 |

## 3.5 DISCUSSION

The sub-surface water pumped from the Sewage Treatment Facility construction site and discharged into St. Lawrence Bay over a 15-month period in this study had detectable effects on environmental conditions, particularly water quality conditions, at the seagrass sites in the Bay. Before the discharge event, there was little association among the different environmental variables across the sites, and little indication that variation in the environmental variables across the sites was affecting variation in the seagrass variables (Figure 3.2). During discharge, there was much stronger association among the environmental variables across the sites (Figure 3.3), implying that there were sites of generally higher environmental quality and sites of generally lower environmental quality.

The most conspicuous and strongest effect of plume discharge was on turbidity of the water column when the plume passed over the sites, with mean values ranging from 27.8 to 74.6 NTU (Table 3.14). These values are well in excess of those (~ 9 NTU) suggested by Thayer *et al.* (1994) based on work by Alleman (1991), as causing light limitation in seagrasses even at water depths of about 1 m. If the seagrasses in St. Lawrence Bay had been continuously subjected to these turbidity values over the 15-month period of discharge, it is unlikely that any would have survived. However, the plume was typically discharged for about 4 hours per day, and the sites varied in terms of their probability of contact with the plume during discharge. Estimated daily contact durations of the plume with the sites are shown in Table 3.1. A likely impact of the plume on seagrasses in St. Lawrence Bay is therefore reductions in length of time that the plants are exposed to appropriate levels of light (see Dennison and Alberte 1985, 1986 and Zimmerman *et al.* 1991 for effects of this on seagrass growth and survival).

Consistent with the high turbidity values observed, suspended particulate matter in the water column was appreciably higher during discharge than before discharge in this study (Table 3.14), and turbidity levels were strongly associated with SPM levels across the sites during discharge. SPM levels during discharge were below those suggested by Dennison *et al.* (1993) as levels at which there may be negative impacts on seagrass beds (~ 15 mg $l^{-1}$). However, Fonseca *et al.* (1998) emphasise that the water quality guidelines provided by Dennison *et al.* (1993) may be useful for temperate seagrass systems, but are likely to be too high for seagrass systems in more oligotrophic tropical and subtropical waters. The high turbidity values, but more modest SPM values, observed in this study suggest that, as might be expected in mangrove-associated water, color was a major contributor to turbidity in the discharged plume.

Consistent with the elevated SPM levels observed, sedimentation rates were significantly higher during discharge than after discharge, but this was not true for all sites (Table 3.15), and sedimentation rates were not well associated with SPM levels across the sites during discharge (Figure 3.3). Tolerance of seagrasses to sedimentation is presumably quite high, since an important function of seagrasses in coastal areas is to trap and bind sediments (Scoffin 1970; Ward *et al.* 1984). There are no published tolerance thresholds for sedimentation rates for seagrasses. However, using silt and clay content of the sediment as an index of sedimentation rate, Terrados *et al.* (1998) reported sharp impacts on seagrass communities when the silt and clay content exceeded 15 %. Bach *et al.* (1998) emphasised the need for further knowledge of tolerance thresholds for sedimentation rates for seagrass systems. Organic content of the sediment was also higher during the discharge period than after discharge in this study, indicating a detectable contribution of the plume to the local sediment regime. However, even during the discharge period, the organic content of the sediment was not particularly high. Allard (1993) provides data indicating that percent organic content of the sediment at nearshore sites in Barbados typically ranges from about 2.3 to about 7.8 (compare this with values in Table 3.15).

Salinity values were lower during discharge than before discharge in this study, but the differences were small (Table 3.14) and were not statistically detectable. The salinity values during discharge were well within the range considered optimal for *Thalassia testudinum* and

*Syringodium filiforme* (25 - 30 $^{o}/_{oo}$; Zieman 1982, Zieman and Zieman 1989, Fonseca *et al.* 1998 for review), and it is therefore most unlikely that salinity changes during discharge could have resulted in any negative impacts on seagrasses in St. Lawrence Bay.

Nitrate concentrations in the water column were higher during discharge than before discharge, but differences in phosphate concentrations were not detectable. The inability to detect phosphate differences need not imply that the plume was not a phosphorous source for seagrasses in the Bay. It should be noted that organic phosphorous was not measured in the study, and could have been at significant levels in the plume. Beyond this, the rapid uptake rate of soluble nutrients, such as inorganic phosphate, in many coastal systems ensures that they are poor indicators of the nutrient status of the system, and this should be particularly true for the limiting nutrient (Smith *et al.* 1981; Valiela *et al.* 1990; Tomasko *et al.* 1996). Moreover, inorganic phosphate is expected to adsorb stongly to the carbonate sediments characteristic of the St. Lawrence site, and this may decrease the probablity of detecting elevated levels in the water column. Interestingly, there are data to suggest that phosphorous may currently be more limiting than nitrogen for *Thalassia* in Barbados (Chapter 1), which is consistent with the inability to detect increases in soluble inorganic phosphates in the water column during the discharge period. An increase in nutrient input could have either a positive effect on seagrass growth and abundance in St. Lawrence Bay, since seagrasses in Barbados are considered to be nutrient-limited (see Patriquin 1972; Chapter 1 this thesis), or negative effects arising through increases in phytoplankton or epiphyte abundance. Negative effects on *Thalassia* growth and abundance were observed during discharge in this study.

The discharge plume was a nutrient source to the Bay and chlorophyll-*a* concentrations were positively associated with nitrate and phosphate levels across the sites during discharge, but chlorophyll-*a* concentrations in the water column did not differ significantly before and during discharge. This indicates that the depressed *Thalassia* growth and abundance observed during discharge cannot be attributed to increased phytoplankton abundance in the water column. Increases in phytoplankton abundance, and hence chlorophyll-*a*, in response to nutrient enrichment may have been constrained by the poor water clarity that characterised the discharge period. Similarly, epiphyte biomass on *Thalassia* leaves, although showing substantial temporal and spatial variation during the study, did not differ before and during the discharge period, and was not well associated with either the water quality variables or the seagrass variables during discharge. Tomasko and Lapointe (1991) have suggested that reduced irradiance can moderate the effect of nutrient enrichment on epiphyte levels on *Thalassia*, and Fitzpatrick and Kirkman (1995) have shown that epiphyte biomass on *Posidonia australis* decreases under shading stress. Frankovich and Fourqurean (1997) showed that effects of nutrient enrichment on epiphyte levels on *Thalassia* were highly localised, and concluded that epiphyte levels may not be as sensitive to moderate nutrient enrichment as other seagrass parameters. Given the ephemeral nature of epiphytes observed in this study, the fact that epiphyte levels did not increase during the discharge period, and the fact that epiphyte levels were not well associated with the seagrass variables during discharge, the negative impacts on *Thalassia* growth and abundance observed during the discharge period can not be attributed to epiphyte effects. Since the negative impacts on *Thalassia* observed during discharge cannot be attributed to either phytoplankton or epiphyte effects, they cannot be attributed to the increased nutrient input to the Bay, but are more likely to result from the high turbidity levels generated during discharge.

*Thalassia* abundance, both as shoot density and as biomass per substrate area, decreased significantly during the 15-month discharge event in St. Lawrence Bay, with the greatest abundance losses occurring at those sites with the highest estimated plume impact indices. Recovery of *Thalassia* was relatively rapid, with significant increases in abundance being detectable 5 months after discharge had ceased. Given the environmental changes which accompanied discharge described above, it seems likely that the *Thalassia* abundance losses resulted primarily from reduced exposure to appropriate irradiance levels. This is supported by the strong negative association between turbidity and area-specific *Thalassia* abundance observed across the sites during the discharge event (Figure 3.3). Fitzpatrick and Kirkman (1995) have shown significant decreases in shoot density of *Posidonia australis* in response to experimental shading, but in contrast to the present results, detected no significant recovery 17 months after shading had ceased. Both Czerny and Dunton (1995) and Lee and Dunton (1997) documented sharp abundance losses in *Thalassia testudinum* under experimental shading, and the latter conclude that a change in shoot density is an important indicator of chronic underwater stress in *T. testudinum*. Dawes (1998) reported significantly lower shoot densities of *T. testudinum* in deep than shallow beds, supporting the suggestion that *Thalassia* shoot density is sensitive to variation in irradiance. Consistent with the sharp decrease in *Thalassia* shoot density and biomass observed in this study, the area-specific growth variable leaf productivity decreased significantly following discharge, with the greatest decreases occurring at the sites with the highest estimated plume impact indices. Productivity was positively associated with area-specific abundance both before (Figure 3.2) and during (Figure 3.3) discharge, and showed a strong negative association with turbidity during discharge.

Effects of the plume discharge were detected, not only on area-specific *Thalassia* variables, but also on shoot-specific variables. Leaf biomass per shoot decreased significantly during discharge and increased significantly when discharge ceased. This was driven in part by changes in leaves per shoot, which tended to decrease during discharge, but also by changes in leaf size, specifically leaf width. Leaf width decreased significantly during the discharge event, with the percent reduction in leaf width being greatest at sites with the highest estimated plume impact index. Leaf width was negatively associated with the environmental variables across the sites during discharge (Figure 3.3). Lee and Dunton (1997) have reported reduced leaf width in response to experimental shading of *T. testudinum*, and Dawes (1998) documented significantly lower leaf widths in deeper *Thalassia* stands than shallower stands. It is not clear whether this is a general seagrass response. West (1990) suggested that leaf width in *Posidonia australis* either differed little between depths, or was narrower at greater depths; but Dalla Via *et al.* (1998) reported wider leaves in deeper stands of *Posidonia oceanica*.

Maximum leaf length, plastochron interval and leaf growth rate did not change significantly during the discharge event in this study. In contrast to this result, Bulthuis (1983) reported that leaf length of *Heterozostera tasmanica* increased with decreased irradiance, and Lee and Dunton (1997) observed longer plastochron intervals in *Thalassia testudinum* in response to shading. Consistent with the present results, Czerny and Dunton (1995) reported little change in leaf elongation (growth) rates of *Thalassia* and *Halodule wrightii* subjected to different levels of light reduction, and concluded that this variable was a poor indicator of the underwater light environment for these species. Similarly, Bulthuis (1983) found no change in *H. tasmanica* leaf growth rates under reduced irradiance. However, Fitzpatrick and Kirkman (1995) reported lower leaf growth rates in response to shading in *Posidonia australis*, again indicating that the responses of shoot-specific seagrass variables to light stress may be species-specific. The inability to detect significant effects of light stress on *Thalassia* leaf growth rates (Czerny and Dunton 1995; this study) is somewhat surprising given that *Thalassia* growth rates are reported to be lower in deeper than shallower beds (Dawes and Tomasko 1988).

The rate of production of new leaves (PI) did not change during the discharge event, but leaf material on a shoot, as leaves per shoot and particularly as biomass per shoot, declined during discharge and was negatively associated with turbidity levels across the sites during discharge (Figure 3.3). The reduction in biomass per shoot in the absence of a PI response implies that the rate of leaf loss increased during discharge, which raises the possibility that average leaf age declined. Since leaf growth rate is higher in younger than older leaves in *Thalassia* (Brouns 1985; van Tussenbroek 1995), any tendency for leaves to grow slower as a consequence of light stress could be buffered by an age-dependent tendency to grow faster, resulting in an inability to detect reduced growth under conditions of light stress if leaf mortalities are higher. This situation of decreasing leaf age may not apply in circumstances where effects of light on leaf growth rate are investigated by comparisons of leaf growth rates in equilibrium *Thalassia* stands at different depths, perhaps explaining why reduced growth rates are detectable at greater depths in such studies.

Relative leaf growth rates and specific leaf productivity rates (i.e. the 2 indices of rate of production of new leaf material per unit of leaf material present) increased during the discharge event and decreased when discharge ceased. The fact that these variables responded differently during discharge to the other growth and abundance *Thalassia* variables is evident in Figure 3.3. This increase in relative growth rate and specific productivity rate cannot be the consequence of changes in production rate of new leaves since PI did not change during discharge. However, it could result from a shift in leaf age structure towards younger leaves. The rate of addition of new material to a leaf per unit of old material present is substantially higher for young leaves than old leaves, which would result in significantly higher relative leaf growth rates and specific leaf productivity rates in the former.

*Thalassia* shoot density, biomass per substrate area, biomass per shoot, leaf productivity, relative leaf growth rate, specific leaf productivity rate and leaf width all changed rapidly and significantly under the environmental stress imposed by the discharge event in this study, and in this sense could all be considered potentially valuable indicators of *Thalassia* condition. Of these variables, shoot density, biomass per substrate area and leaf width showed reductions that were significantly correlated with the estimated severity impact of the plume at the sites, and also showed a reversal of their loss trends when the discharge ceased. This suggests that these variables are particularly responsive to the environmental stress imposed. Shoot density and leaf width offer the additional advantage of being easy to measure in the field, with negligible impacts on the seagrass plants. Moreover, leaf width did not vary seasonally, and shoot density showed only a weak seasonal effect in this study (Chapter 1; but note that leaf width does increase with shoot age, Chapter 2).

On the basis of responsiveness to environmental stress, ease of measurement, and negligible seasonal effects (Chapter 1, this thesis), shoot density and leaf width should be considered priority variables to include as indicators of seagrass condition in *Thalassia* monitoring programs in tropical areas. Based on their sensitivity and rapid response to changes in underwater irradiance, Lee and Dunton (1997) also identified shoot density and leaf width (but also PI) as valuable indicators of *Thalassia* condition; and Fitzpatrick and Kirkman (1995) recommended that shoot densities (but also leaf growth rates) should be used to monitor the health of *Posidonia australis* meadows.

In contrast to the abundance losses observed in *Thalassia*, *Syringodium* shoot density increased at most sites during the discharge event. Only at Site 5, the *Syringodium* site with the highest plume impact index, was *Syringodium* shoot density clearly lower during discharge than before discharge (Table 3.13). Two important inferences can be drawn from the tendency of *Syringodium* abundance to increase during the discharge event. The first is that it supports the contention (see Williams 1990; Fourqurean *et al.* 1995) that later colonisers replace earlier colonisers in the seral development of seagrass communities in the Caribbean because the latter are more effective competitors for sediment nutrients, i.e. they can draw down sediment nutrient availability below the requirements of earlier colonisers. With additional nutrients made available through plume discharge, and through the reduced abundance of *Thalassia*, *Syringodium* abundance increased. This second effect may have been stronger than the first in increasing *Syringodium* abundance. *Syringodium* abundance showed a strong negative association with *Thalassia* abundance across the sites during the discharge event, but also showed a negative association with nutrient levels in the water column (Figure 3.3). The latter would not be expected if the increased water column nutrients were the principal cause of *Syringodium* abundance increases.

The second inference from the *Syringodium* changes observed is that *Syringodium* has lower light requirements than *Thalassia*, since *Syringodium* abundance increased under the conditions of impaired irradiation that are suggested to have decreased *Thalassia* abundance. Based on distributional data, Buesa (1974) and Zieman *et al.* (1989) have suggested that *Syringodium* has lower light requirements than *Thalassia*, and Buesa (1974) reported lower compensation light intensities for *Syringodium* leaf photosynthesis than for *Thalassia* leaf photosynthesis. Only at Site 5 did light conditions appear to have been severe enough to reduce *Syringodium* abundance. Based on these results, it seems likely that a typical effect of coastal eutrophication will be to reverse the seral development of seagrass colonisation from *Thalassia* to *Syringodium*. Eutrophication can impair water column transparency, thereby leading to abundance decreases in *Thalassia*; and this, along with the direct nutrient effects of eutrophication, can increase nutrient availability to *Syringodium*. A reversal of the seral development of seagrass colonisation from *Thalassia* to *Halodule wrightii* in response to eutrophication has previously been reported by Lapointe *et al.* (1994) and Fourqurean *et al.* (1995). The latter suggest that the increase in *Halodule* abundance resulted from increased sediment nutrient availability, and that the decrease in *Thalassia* abundance resulted from decreased light availability. They suggested that *Halodule* was the more effective competitor for light both through having a lower light requirement than *Thalassia* (see also Wiginton and McMillan 1979; Iverson and Bittaker 1986; Fourqurean and Zieman 1991), and through more effectively blocking *Thalassia*'s access to light by the formation of dense canopies of "aerial runners". It is important to note that the suggestion in this study that *Syringodium* can increase in abundance relative to *Thalassia* under conditions of impaired irradiance potentially contradicts the suggestion of Williams (1987, 1990) that *Thalassia* is a better competitor than *Syringodium* for light. Williams (1987) reported an increase in *Syringodium* abundance when the *Thalassia* leaf canopy was removed. This demonstrates the existence of light competition between the two species, but does not in itself indicate which of the species is the better light competitor. Williams (1987) did not conduct the reverse experiment, i.e. assessing changes in *Thalassia* abundance when the *Syringodium* leaf canopy was removed (see Chapter 4 this thesis).

It is of interest to view the question of whether *Thalassia* or *Syringodium* may be the more effective light competitor, at least in the sense of having the lower light requirement, in the context of the resource ratio hypothesis of Tilman (1985, 1987, 1988). An important contention of this hypothesis is that characteristics which allow a species to be an effective competitor for one category of limiting resource are likely to constrain its effectiveness in competing for a second category of limiting resource. Consequently, a given species can not be categorised as either a poor competitor or a superior competitor, but its competitive capacity depends on the resource for which it is competing. In the context of competition between *Thalassia* and *Syringodium*, the important questions may not be which species has the lower light requirement or which species has the higher nutrient requirement. There is indeed no *a priori* reason for assuming an intrinsic biochemical or physiological difference between the two species such that they necessarily differ in terms of the amount of light required to support a given unit of biomass, or the amount of nutrients required to support a given unit of biomass. In the context of competition for light and nutrients, the more appropriate questions may be which species has the higher capacity to obtain light per unit of biomass to support, and which species has the higher capacity to obtain and store nutrients per unit of biomass to support. An important difference between *Thalassia* and *Syringodium* suggested by data reported in the literature and explored further in Chapter 4 (this thesis), is that *Thalassia* has a substantially higher ratio of belowground biomass (rhizomes and roots) to aboveground biomass (leaves). The values reported range from about 5:1 to 10:1 for *Thalassia* and from 1.3:1 to 3.3:1 for *Syringodium* (Williams 1987, 1990; Powell *et al.* 1989; Short *et al.* 1993). This implies that *Thalassia* has the higher capacity to obtain and store sediment nutrients per unit of total biomass to support, and may largely explain why *Thalassia* can retain biomass levels better than *Syringodium* as available sediment nutrients decline. This very characteristic which allows *Thalassia* abundance to increase relative to *Syringodium* abundance as nutrient availability declines may itself ensure that *Thalassia* abundance will decrease relative to *Syringodium* abundance as light availability declines. By virtue of its higher ratio of leaf biomass to root and rhizome biomass, *Syringodium* will have a higher capacity than *Thalassia* to obtain light per unit of total biomass to support, and will therefore be able to retain biomass levels better than *Thalassia* as available light declines. Consistent with these contentions, Fourqurean *et al.* (1995) commented that the trade-offs between accumulation of light and accumulation of nutrients determine the behavior of *T. testudinum* and *H. wrightii* in Florida Bay; and Hemminga (1998) has emphasised that the root and rhizome system of a seagrass plant is the component that critically determines the plant's vulnerability to light reduction. Iverson and Bittaker (1986) had earlier suggested that the compensation light level for *Thalassia* is greater than that for *Syringodium* and *Halodule* because of the respiration demands created by the greater proportion of non-photosynthetic tissue in *Thalassia*; and Duarte (1991) observed that the deepest seagrass communities are dominated by species with small rhizomes, which should therefore have small respiratory demands. These observations suggest that the simple ratio of leaf biomass to root and rhizome biomass in seagrasses may be a strong predictor of the likely outcome of competition for both nutrients and light; and therefore a strong predictor of both the typical successional sequence of seagrasses under conditions of decreasing nutrient availability, and the reversal sequence of seagrasses under conditions of enhanced nutrients and impaired light.

# CHAPTER 4 LIGHT AND NUTRIENT COMPETITION IN TWO CARIBBEAN SEAGRASSES, *THALASSIA TESTUDINUM* AND *SYRINGODIUM FILIFORME*

## 4.1 ABSTRACT

Light and nutrient competition between *Thalassia testudinum* and *Syringodium filiforme* was investigated in St. Lawrence Bay, Barbados. Two principal experiments, the Nutrient Experiment and the Light Experiment, were conducted, and several field observations relevant to the question of nutrient competition between *Thalassia* and *Syringodium* were documented. In the Nutrient Experiment, sediment nutrient levels were manipulated by fertilisation, and the growth responses of *Syringodium* and *Thalassia*, as productivity per shoot and specific leaf productivity rate, were compared. *Syringodium* showed a greater growth response to fertilisation than *Thalassia*. This suggests that *Syringodium* growth may be more suppressed than *Thalassia* growth by limited nutrient availability, and hence that *Thalassia* may be more effective than *Syringodium* at using limited sediment nutrients. Total biomass per $m^2$ of *Thalassia* in monospecific stands was significantly higher than that of *Syringodium*, and leaf nitrogen and phosphorous content was higher for *Thalassia*. This supports the suggestion that *Thalassia* has a higher capacity to obtain sediment nutrients and hence to support plant biomass than does *Syringodium* in a nutrient-limited environment. Biomass per shoot, productivity per shoot and specific leaf productivity rate were higher for *Thalassia* in mixed stands than monospecific stands suggesting that nutrient competition is more extreme for *Thalassia* in the latter stands. Productivity per shoot and specific leaf productivity rate tended to be lower for *Syringodium* in mixed than monospecific stands in an unfertilised environment, but the differences between stand types were not statistically significant. In the Light Experiment, light levels were manipulated by canopy removal, and effects of *Thalassia* canopy removal on *Syringodium* growth and of *Syringodium* canopy removal on *Thalassia* growth (growth as leaf growth

rate, specific leaf productivity rate and productivity per shoot) were assessed. The results indicate that *Syringodium* inhibits *Thalassia* growth through light competition more than *Thalassia* inhibits *Syringodium* growth, suggesting that *Syringodium* is the more effective light competitor. *Thalassia* has a higher belowground to aboveground biomass ratio than *Syringodium*. This provides *Thalassia* with a potentially higher capacity to obtain and store sediment nutrients per unit of total biomass to support, and provides *Syringodium* with a potentially higher capacity to obtain light per unit of total biomass to support. This morphological difference may largely explain why *Thalassia* is the more effective nutrient competitor and *Syringodium* the more effective light competitor. The results suggest that seagrasses in St. Lawrence Bay may be constrained by both nutrient competition and light competition, and may move between nutrient and light limitation over relatively small spatial scales. Since *Thalassia* appears to be the more effective nutrient competitor and *Syringodium* the more effective light competitor, this situation may largely explain the coexistence of species commonly observed in Caribbean seagrass communities.

## 4.2 INTRODUCTION

The typical sequence of seagrass colonisation in the Caribbean is accepted to be from rhizophytic green macroalgae, to the seagrasses *Halodule wrightii* and/or *Syringodium filiforme* to *Thalassia testudinum* (den Hartog 1971; Zieman 1976; Williams 1987, 1990), but uncertainty remains over the processes underlying the successional changes. An emerging consensus is that early colonisers precede later colonisers because they have higher leaf and rhizome growth rates and can therefore more rapidly colonise open spaces (Gallegos *et al.* 1994; Fourqurean *et al.* 1995; see also Gleeson and Tilman 1990, Tilman and Wedin 1991 for a similar perspective in terrestrial plant succession). Consistent with their faster growth, early colonisers in marine plant communities are believed to have higher nutrient demands than later colonisers, where nutrient demand is a measure of the rate at which the plant incorporates nutrients into plant biomass (Fourqurean *et al.* 1995; Pedersen and Borum 1997). A switch from high to low resource demands may be a general characteristic of terrestrial plant succession (Bazzaz 1979).

The high nutrient demand of early seagrass colonisers is suggested to be the cause of their subsequent suppression. Fourqurean *et al.* (1992, 1995) demonstrate a higher nutrient demand in *Halodule wrightii* than *Thalassia testudinum*, conclude that *Halodule* requires more nutrients than *Thalassia*, and suggest that *Thalassia* draws down sediment nutrient availability below *Halodule*'s requirements. The suggestion that *Halodule* requires more nutrients than *Thalassia* is supported by studies documenting an increase in the relative abundance of *Halodule* to *Thalassia* in response to eutrophication (Powell *et al.* 1991; Lapointe *et al.* 1994; Fourqurean *et al.* 1995). Nutrient interactions between *Syringodium* and *Thalassia* have received less attention, but Williams (1987, 1990) suggested that *Thalassia* suppresses *Syringodium* in the seagrass successional sequence because it is the more effective nutrient competitor, which may imply that it has the lower nutrient requirement. The generality of the contention that it is the high nutrient demand of earlier colonisers that underlies their subsequent suppression in the Caribbean successional sequence is constrained by the absence of studies on nutrient demand in *Syringodium*. It should be noted that a potential paradox in seagrass succession is the contention that nutrient pools increase as succession proceeds (Williams 1990; Fourqurean *et al.* 1992; see also Tilman 1982), but that early colonisers have high nutrient demands and late colonisers have low nutrient demands. The issue is resolved with the acceptance that, although the total nutrient pool in the seagrass system increases over time, the abundance of available sediment nutrients decreases, at least over the later successional stages. In contrast to the emphasis on nutrient demand, it was suggested in Chapter 3 that later colonisers (e.g. *Thalassia*) may be able to suppress later colonisers (e.g. *Syringodium*) as succession proceeds and available nutrients become more limiting because they have higher belowground to aboveground biomass ratios.

The role of light competition in seagrass succession is more controversial than nutrient competition (see Kenworthy and Schwarzschild 1998). One might expect light availability to decrease as succession proceeds and plant biomass increases (Williams 1987). Ideally, later colonisers should therefore be better competitors for light. Consistent with this, Williams (1987) concluded that *Thalassia* could inhibit *Syringodium* by reducing light availability and that *Thalassia* was therefore the better competitor for light. In contrast to Williams' claim that the later coloniser is a more effective light competitor than the earlier coloniser, Fourqurean *et al.* (1995) conclude that the earlier coloniser *Halodule* is a better competitor for light than *Thalassia*, despite the fact that light availability may decrease as succession proceeds, both because *Halodule* has a lower light requirement than *Thalassia* and because *Halodule* can block *Thalassia*'s access to light by the formation of dense canopies of "aerial runners". In Chapter 3, it was suggested that earlier colonisers (e.g. *Syringodium*) may be able to suppress later colonisers (e.g. *Thalassia*) in light competition because they have higher aboveground to belowground biomass ratios.

The observation that *Thalassia* growth and abundance decreased and *Syringodium* abundance increased in response to the discharge event described in Chapter 3 is pertinent to understanding competitive interactions between the species and the changes that occur as succession proceeds or reverses. The decline in *Thalassia* growth and abundance was suggested to result primarily from reduced light following increased turbidity. The fact that *Syringodium* abundance increased under the same light conditions may suggest that it has lower light requirements than *Thalassia*, and raises the possibility that it is the more effective light competitor. Only Williams (1987) has experimentally investigated light competition between *Thalassia* and *Syringodium*. She documented an increase in *Syringodium* abundance when the *Thalassia* leaf canopy was removed, and concluded that *Thalassia* could inhibit *Syringodium* by reducing light availability and was therefore the better competitor for light. Williams (1987) did not assess changes in *Thalassia* abundance when *Syringodium* leaf canopy was removed. Her experiment can therefore confirm the existence of light competition between *Syringodium* and *Thalassia*, but can not definitively indicate which species is the better light competitor. The latter would require an assessment of the magnitude of response of both species to a release from interspecific light competition.

The increase in *Syringodium* abundance reported in Chapter 3 was suggested to result primarily from increased nutrient availability following the decrease in *Thalassia* abundance. The explanation assumes the existence of nutrient competition between *Thalassia* and *Syringodium*, but the observed response of *Syringodium* does not allow explicit determination of which species is the better nutrient competitor. The latter would require an assessment of the magnitude of response of both species to a release from interspecific nutrient competition. Relative responses of *Thalassia* and *Syringodium* to experimental manipulation of sediment nutrient levels have not been reported.

In this study, I conducted two principal experiments and documented several field observations pertinent to the issue of nutrient and light competition between *Thalassia* and *Syringodium*. In one experiment (the Light Experiment), light availability to each species was manipulated by removing the leaf canopy of the other. The hypothesis is that, if *Syringodium* and *Thalassia* are in competition for light and *Syringodium* is the more effective light competitor, *Syringodium* should suppress *Thalassia* growth to a greater extent than

*Thalassia* suppresses *Syringodium* growth. The testable prediction is that, when released from the interspecific light competition, *Thalassia* should show a greater growth response than *Syringodium*.

In the second experiment (the Nutrient Experiment), sediment nutrient availability to *Thalassia* and *Syringodium* was manipulated by fertiliser addition. The hypothesis is that, if *Thalassia* and *Syringodium* are in competition for sediment nutrients and *Thalassia* is the more effective nutrient competitor, *Thalassia* should suppress *Syringodium* growth to a greater extent than *Syringodium* suppresses *Thalassia* growth. The testable prediction is that, when released from the interspecific nutrient competition, *Syringodium* should show a greater growth response than *Thalassia*.

The field observations, which include direct field measurements as well as additional information emerging from the Nutrient Experiment, can be placed in two broad categories; namely, those designed to supplement the assessment of whether *Thalassia* is a more effective competitor for sediment nutrients than *Syringodium* (Items 1-4 below), and those designed to provide comment on reasons why *Thalassia* may be the more effective competitor for nutrients and *Syringodium* the more effective competitor for light (Items 5 and 6 below). It is important to appreciate that these field observations must be perceived as only indicative of the relative effectiveness of the 2 species as nutrient competitors, and only indicative of the possible mechanisms determining their effectiveness as competitors. The observations do not provide definitive proof of the relative effectiveness of the 2 species in obtaining sediment nutrients, or of the mechanisms underlying their effectiveness. The field observations made are described below.

(1) The total biomass per m$^2$ of *Thalassia* and *Syringodium* in monospecific stands in the primarily nutrient-limited environment of St. Lawrence Bay was compared. A greater biomass per m$^2$ for *Thalassia* than *Syringodium* would be consistent with the contention that *Thalassia* is more effective at obtaining sediment nutrients.

(2) Leaf biomass per shoot was compared in monospecifc and mixed stands of *Thalassia* and *Syringodium*. A smaller biomass per shoot of *Thalassia* in monospecific than mixed stands would be consistent with *Thalassia* being more effective at obtaining sediment nutrients, since nutrient competition should be more extreme for *Thalassia* in monospecific stands. A smaller biomass per shoot of *Syringodium* in mixed than monospecific stands would be consistent with *Thalassia* being more effective at obtaining sediment nutrients, since nutrient competition should be more extreme for *Syringodium* in the former stands.

(3) The growth variables leaf productivity per shoot and specific leaf productivity rate were compared in monospecific and mixed stands of *Thalassia* and *Syringodium* in an experimental design which reduced the probability that light was limiting (clipping and regrowth in the Nutrient Experiment). As in (2) above, slower growth of *Thalassia* in monospecific than mixed stands, and slower growth of *Syringodium* in mixed than monospecific stands, would be consistent with *Thalassia* being more effective than *Syringodium* at obtaining sediment nutrients. This experiment was repeated in a nutrient-enriched environment (fertiliser addition) to determine whether any differences detected between monospecific and mixed stands were lost following nutrient enrichment.

(4) The nitrogen and phosphorous contents of *Thalassia* and *Syringodium* leaves were compared in the growth experiments described in (3) above. Higher concentrations of nitrogen and phosphorous in *Thalassia* than *Syringodium* leaves in the primarily nutrient-limited environment of St. Lawrence Bay would be consistent with the contention that *Thalassia* is more effective at obtaining sediment nutrients.

(5) Nutrient demands of *Thalassia* and *Syringodium* in the growth experiments described in (3) were compared. A lower nutrient demand for *Syringodium* would be inconsistent with the contention that earlier colonisers (e.g. *Syringodium*) are poor nutrient competitors because they have higher nutrient demands than later colonisers (e.g. *Thalassia*; see Section 4.2 for elaboration of contention).

(6) The ratios of belowground to aboveground biomass of *Thalassia* and *Syringodium* were compared. A lower belowground to aboveground biomass ratio for *Thalassia* at the same study site where the nutrient and light competition experiments were conducted would be consistent with the contention that *Thalassia* is the more effective nutrient competitor (and less effective light competitor) because it has a higher belowground to aboveground biomass ratio (see Section 3.5 for elaboration of contention).

## 4.3 METHODS

The study was conducted in St. Lawrence Bay on the south coast of Barbados between June and September 1999 in monospecific and mixed stands of *Thalassia testudinum* and *Syringodium filiforme* (see Chapter 1, Section 1.3 for location and description of site). Data were collected in 2 experiments (the Nutrient Experiment; the Light Experiment) and through field measurements of the biomass of *Thalassia* and *Syringodium* in the different stand types.

### 4.3.1 The Nutrient Experiment

Eight 25 cm x 25 cm (0.0625 $m^2$) quadrats were randomly located and permanently fixed in each of 4 seagrass stands (*Thalassia* monospecific, *Thalassia* mixed, *Syringodium* monospecific, *Syringodium* mixed; note that *Thalassia* mixed and *Syringodium* mixed are the same stand type). All quadrats were at water depths ranging from 0.6 to 0.8 m (MLW). The number of shoots in each quadrat was counted, and all leaves in each quadrat were clipped to substrate level and allowed to regrow for 14 days. The leaves were then reclipped, the initial leaf tissue samples and the leaf regrowth samples rinsed free of sediments and adherent epibionts, and dried at 70 °C for 24 hours or until constant weight. Calcareous epipytes were removed from the initial leaf tissue samples by rinsing the leaves in 5 % phosphoric acid and gently scraping off any remaining carbonate material. Calcareous epiphytes had not formed on the leaf regrowth samples. The data were used to calculate 2 growth indices for each quadrat in each stand. These were leaf productivity per shoot (mg DW $shoot^{-1}$ $d^{-1}$) and specific leaf productivity rate (expressed as mg $g^{-1}$ $d^{-1}$) and calculated as leaf regrowth/initial leaf weight per day.

Following the 14 days of regrowth, the experiment was repeated, but under fertilised conditions. Plots were fertilised for 42 days prior to measurement of the growth indices to allow sediment nutrient accumulation. Slow release fertilisers (90-day release 16-8-8 NPK Jobes tree spikes) were added to each of the plots at a fertilisation rate of 600 g N $m^{-2}$ and 341 g P $m^{-2}$. This application rate approximated that used by Williams (1990) for N, but was more than twice that used for P. At the end of the 56-day period (42 days nutrient conditioning, 14 days of regrowth), portions of the fertiliser spikes remained in the sediment, indicating that fertiliser was available to supply nutrients throughout the experiment. Comparisons of growth in unfertilised and fertilised plots allowed the hypothesis developed in Section 4.2 for the Nutrient Experiment to be tested.

Dried regrowth leaf material from both the unfertilised and fertilised phases of the Nutrient Experiment was ground to a fine powder (for sample homogeneity), and leaf tissue nitrogen and phosphorous content, as % dry weight, was determined separately for each sample from all unfertilised and fertilised plots. Samples were stored in Nalgene sample vials and frozen until analysis. Total leaf nitrogen content was determined at Darling Marine Laboratory, University of Maine, using a CHN analyser; total leaf phosphorous content was determined by Philip Analytical Services Inc. (Canada) using colorimetry following hot acid digestion. These data allowed leaf tissue nitrogen and phosphorous content of *Thalassia* and *Syringodium* leaves to be compared (see Section 4.2, Field Observation 4), and allowed estimates of *Thalassia* and *Syringodium* nutrient demand to be calculated, separately for nitrogen and phosphorous, as the nutrient concentrations x the measured specific leaf productivity rate (see Section 4.2, Field Observation 5).

### 4.3.2 The Light Experiment

Twenty-four 40 cm x 40 cm (0.16 $m^2$) plots were randomly selected and permanently marked in a large, continuous mixed stand of *Thalassia* and *Syringodium* in about 1.2 m (MLW) of water. Two clipping treatments were applied to assess the effects of *Thalassia* on *Syringodium* growth. In the first treatment, the *Thalassia* leaf canopy within each of 6 of the

0.16 $m^2$ plots was clipped to substrate level and *Thalassia* leaf regrowth was measured in the presence of a *Syringodium* leaf canopy (i.e. *Syringodium* canopy not clipped). Regrowth was measured each week for 6 weeks using 1 of the six 0.16 $m^2$ plots on each weekly sampling occasion, i.e. the growth was measured at 7, 14, 21, 28, 35 and 42 days following clipping. In the second treatment, both the *Thalassia* and *Syringodium* leaf canopies within each of 6 of the 0.16 $m^2$ plots were clipped to substrate level, and *Syringodium* was reclipped every second day. *Thalassia* regrowth was therefore measured in the absence of a *Syringodium* leaf canopy. Regrowth was again measured weekly over a 6-week period following initial clipping.

A similar approach was used to assess effects of *Thalassia* on *Syringodium* growth. First, the *Syringodium* leaf canopy within each of six 0.16 $m^2$ plots was clipped and *Syringodium* leaf regrowth was measured in the presence of a *Thalassia* leaf canopy. Secondly, both *Syringodium* and *Thalassia* canopies within each of six 0.16 $m^2$ plots were clipped, and *Thalassia* was reclipped every second day. *Syringodium* regrowth was therefore measured in the absence of a *Thalassia* leaf canopy. For both treatments, regrowth was again measured weekly over a 6-week period following initial clipping.

The growth rate variables measured were average leaf growth rate per shoot (cm $d^{-1}$), leaf productivity per shoot and specific leaf productivity rate (see Section 4.3.1 for measurement units). Leaf growth rate of *Thalassia* was measured on 15 shoots randomly selected from each plot, using a modified leaf marking technique (*sensu* Zieman 1974; see Section 1.3.2.2 for measurement details). Growth rates in *Syringodium* were also measured on 15 shoots from each plot, but total leaf elongation was used since marking techniques are problematic in this species. Leaf productivity per shoot and specific leaf productivity rate were measured on clipped leaf biomass, as described in Section 4.3. Comparisons of the growth data obtained allowed the hypothesis developed for the Light Experiment in Section 4.2 to be tested.

The Light Experiment described above was repeated with fertiliser application, using the same application rates as in the Nutrient Experiment (Section 4.3.1). However, in the fertilised study, leaf regrowth was measured at only 7, 14 and 42 days. The rationale for the fertiliser component of the Light Experiment was to minimise the probability that any differences detected between clipping treatments was due to nutrient competition effects.

### 4.3.3 Field Measurements of Biomass

Eight samples were collected for total biomass from each of 4 stands (*Thalassia* monospecific, *Thalassia* mixed, *Syringodium* monospecific, *Syringodium* mixed) at water depths ranging from 0.6 to 0.8 m (MLW) using a 16 cm diameter PVC corer inserted 0.67 m into the sediment. Shoot densities were determined as the number of shoots in each core sample. Each core was rinsed free of sediments in fresh water and sorted into the different plant components (i.e. leaves, leaf sheaths, roots, rhizomes). Calcareous epiphytes on leaf tissues were removed by rinsing leaves in 5 % phosphoric acid and gently scraping off any remaining carbonate material. The individual plant components were dried at 70 °C for 24 hours, or until constant biomass was reached, to determine biomass for each component. These data allowed total biomass per $m^2$ of *Thalassia* and *Syringodium* in monospecific stands to be compared (see Section 4.2, Field Observation 1); biomass per shoot to be compared in monospecific and mixed stands for both *Thalassia* and *Syringodium* (see Section 4.2, Field Observation 2); and the ratio of belowground to aboveground biomass to be compared for *Thalassia* and *Syringodium* (see Section 4.2; Field Observation 6).

### 4.3.4 Data Analysis

Effects of fertilisation on *Thalassia* and *Syringodium* growth, and differences in growth in monospecific and mixed stands (the Nutrient Experiment), were analysed using

Two-Way Analyses of Variance, with treatment (fertilised vs unfertilised) and stand type (monospecific vs mixed) as the independent variables. Differences between *Thalassia* and *Syringodium* in leaf nutrient content and nutrient demand (the Nutrient Experiment) were also analysed using Two-Way Analyses of Variance, but with species (*Thalassia* vs *Syringodium*) and treatment (fertilised vs unfertilised) as the independent variables.

Effects of clipping of *Syringodium* leaves on *Thalassia* growth, and of clipping of *Thalassia* leaves on *Syringodium* growth (the Light Experiment) were analysed using Two-Way Analyses of Variance with treatment (competitor's leaves clipped vs not clipped) and time as the independent variables. These ANOVAs were conducted separately for the unfertilised Light Experiment and fertilised Light Experiment, and were supplemented by Two-Sample t-tests assessing growth differences between clipped and unclipped treatments separately for each time period following clipping.

Comparisons of *Thalassia* biomass in monospecific and mixed stands, and of *Syringodium* biomass in monospecific and mixed stands, were conducted using Two-Sample t-tests.

## 4.4 RESULTS

### 4.4.1 Nutrient Competition

#### 4.4.1.1 *Effects of Fertilisation on Growth of Thalassia and Syringodium*

There was a significant effect of stand type (monospecific vs mixed stands) on *Thalassia* productivity per shoot (Two-Way Analysis of Variance: F=7.34, P<0.02; see Section 4.4.1.2), but no effect of fertilisation (F=0.02, P=0.90) and no interaction between stand type and fertilisation (F=0.75, P=0.40) (Table 4.1). Similarly, there was a weak effect of stand type on specific leaf productivity rate of *Thalassia* (F=2.76, P=0.09; see Section 4.4.1.2), but no effect of fertilisation (F=0.15, P=0.71) and no interaction between stand type and fertilisation (F=0.08, P=0.80) (Table 4.1). By contrast, there was a significant effect of fertilisation on *Syringodium* productivity per shoot (F=10.64, P<0.003; productivity higher following fertilisation; Table 4.1), but no effect of stand type (F=0.01, P=0.91) and no interaction between fertilisation and stand type (F=0.07, P=0.80) (Table 4.1). Moreover, there was a significant effect of fertilisation on specific leaf productivity rate of *Syringodium* (F=10.21, P<0.003; productivity higher following fertilisation; Table 4.1), but no effect of stand type (F=0.83, P=0.37; see Section 4.4.1.2) and no interaction between fertilisation and stand type (F=1.28; P=0.27).

These results indicate a greater growth response of *Syringodium* than *Thalassia* when the species are freed of nutrient competition by fertilisation, suggesting that *Syringodium* growth is typically more suppressed than *Thalassia* growth by limited nutrient availability. This in turn suggests that *Thalassia* is more effective than *Syringodium* at obtaining sediment nutrients when nutrient availability is low, and hence that *Thalassia* may be the more effective nutrient competitor.

**Table 4.1.** Productivity per shoot and specific leaf productivity rate of *Thalassia* and *Syringodium* in unfertilised and fertilised monospecific and mixed stands. Values are means (N=8 quadrats) ± standard errors.

| | **UNFERTILISED** | | | | **FERTILISED** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Monospecific** | | **Mixed** | | **Monospecific** | | **Mixed** | |
| | **Mean** | **± SE** | **Mean** | **± SE** | **Mean** | **± SE** | **Mean** | **± SE** |
| ***Thalassia testudinum*** | | | | | | | | |
| Productivity per shoot (mg DW shoot$^{-1}$ d$^{-1}$) | 4.96 | 0.63 | 7.5 | 0.85 | 5.67 | 0.61 | 6.98 | 0.72 |
| Specific Leaf Productivity Rate (mg g$^{-1}$ d$^{-1}$) | 24.36 | 2.28 | 29.85 | 4.15 | 26.24 | 1.24 | 30.13 | 2.81 |
| ***Syringodium filiforme*** | | | | | | | | |
| Productivity per shoot (mg DW shoot$^{-1}$ d$^{-1}$) | 0.61 | 0.04 | 0.51 | 0.04 | 1.41 | 0.35 | 1.45 | 0.40 |
| Specific Leaf Productivity Rate (mg g$^{-1}$ d$^{-1}$) | 23.60 | 3.15 | 18.72 | 2.69 | 28.55 | 1.35 | 29.08 | 1.99 |

### 4.4.1.2 *Growth of Thalassia and Syringodium in Monospecific and Mixed Stands*

There was a significant effect of stand type on *Thalassia* productivity per shoot (see Section 4.4.1.1), with values being higher in mixed than in monospecific stands (Table 4.1; see Section 4.2, Field Observation 3). This supports the suggestion that nutrient competition experienced by *Thalassia* is more extreme in monospecific than mixed stands.

There was a significant effect of stand type on specific leaf productivity rate of *Thalassia* (see Section 4.4.1.1), with values being higher in mixed than monospecific stands (Table 4.1). This again supports the suggestion that nutrient competition experienced by *Thalassia* is more extreme in monospecific than mixed stands.

There was no effect of stand type on either *Syringodium* productivity per shoot or on *Syringodium* specific leaf productivity rate (see Section 4.4.1.2). However, it may be worth noting that the values of both variables were lower in mixed than monospecific stands in an unfertilised environment, but not in a fertilised environment (Table 4.1). This weakly supports the suggestion that nutrient competition experienced by *Syringodium* is more extreme in mixed than monospecific stands.

### 4.4.1.3 *Biomass of Thalassia and Syringodium in Monospecific and Mixed Stands*

The total biomass per m$^2$ of *Thalassia* in monospecific stands was significantly higher than the total biomass per m$^2$ of *Syringodium* in monospecific stands (Table 4.2; Two-Sample t-test: $t=3.23$, $P<0.006$). Since seagrasses in Barbados are typically nutrient-limited (Chapters 1,3 this thesis; Patriquin 1972), the ability of *Thalassia* to maintain a higher biomass than *Syringodium* is consistent with the suggestion that the former is more effective at obtaining sediment nutrients (see Section 4.2, Field Observation 1). The total biomass per m$^2$ of *Thalassia* in mixed stands was also higher than the total biomass per m$^2$ of *Syringodium* in

**Table 4.2.** Biomass (g DW $m^{-2}$) of *Thalassia* and *Syringodium* in monospecific and mixed stands, presented separately for different plant components. % leaf is percent leaf biomass of total biomass; % root is percent root biomass of total biomass. Values are means of 8 cores (0.02 $m^2$) ± standard errors.

| PLANT COMPONENT | *THALASSIA TESTUDINUM* | | | | *SYRINGODIUM FILIFORME* | | | |
|---|---|---|---|---|---|---|---|---|
| | **Monospecific** | | **Mixed** | | **Monospecific** | | **Mixed** | |
| | **Mean** | **± SE** | **Mean** | **± SE** | **Mean** | **± SE** | **Mean** | **± SE** |
| Leaves | 207.08 | 12.08 | 115.41 | 19.16 | 302.06 | 59.18 | 177.84 | 17.84 |
| Leaf Sheaths | 136.96 | 6.58 | 78.80 | 13.37 | 146.37 | 26.71 | 89.53 | 8.24 |
| Leaf : Leaf Sheath | 1.51 | 0.03 | 1.48 | 0.06 | 2.03 | 0.06 | 1.98 | 0.10 |
| **Aboveground Biomass** | 344.04 | 18.42 | 194.21 | 32.36 | 448.43 | 85.78 | 267.37 | 25.53 |
| Rhizomes (horizontal + vertical) | 1703.80 | 80.31 | 872.49 | 170.37 | 1019.27 | 193.95 | 623.60 | 50.78 |
| Roots | 639.76 | 35.84 | 292.55 | 62.72 | 163.78 | 33.27 | 108.36 | 11.65 |
| Rhizome : Root | 2.70 | 0.14 | 3.07 | 0.12 | 6.53 | 0.76 | 5.91 | 0.35 |
| **Belowground Biomass** | 2343.56 | 104.01 | 1165.04 | 232.79 | 1183.05 | 220.97 | 731.96 | 60.55 |
| **Total Biomass** | 2687.60 | 118.04 | 1359.25 | 264.58 | 1631.48 | 304.83 | 999.33 | 85.99 |
| **Belowground : Aboveground** | 6.87 | 0.25 | 5.82 | 0.33 | 2.64 | 0.12 | 2.76 | 0.04 |
| **% Leaf** | 7.71 | | 8.49 | | 18.51 | | 17.80 | |
| **% Root** | 23.80 | | 21.52 | | 10.04 | | 10.84 | |
| **Leaf Biomass per shoot** | 0.25 | 0.08 | 0.37 | 0.12 | 0.03 | 0.01 | 0.03 | 0.01 |

mixed stands (Table 4.2), but the difference was not statistically significant, given the high variance in *Thalassia* and *Syringodium* biomass in mixed stands (t=1.29, P=0.22).

Leaf biomass per shoot of *Thalassia* was significantly higher in mixed stands than monospecific stands (Table 4.2; t=2.30, P<0.04), suggesting that inhibition of *Thalassia* through intraspecific competition in monospecific stands is greater than the inhibition of *Thalassia* when competitive effects are partially conspecific and partially interspecific with *Syringodium* (see Section 4.2, Field Observation 2). This supports the suggestion that *Thalassia* is more effective at obtaining sediment nutrients, and hence of suppressing growth of competitors, than is *Syringodium*. In contrast to expectations, leaf biomass per shoot of *Syringodium* did not differ between monospecific and mixed stands (Table 4.2; t=0.38, P=0.71).

### 4.4.1.4 *Leaf Nutrient Content*

In monospecific stands, there was a significant effect of species on leaf nitrogen content (Two-Way Analysis of Variance; F=111.74, P<0.001; *Thalassia* > *Syringodium*; Table 4.3), a significant effect of fertilisation (F=150.07, P<0.001; values higher following fertilisation; Table 4.3) and a significant interaction effect (F=5.94, P<0.02), which indicates that the magnitude of the increase in nitrogen content following fertilisation differed between species. The results were similar in mixed stands. There was again a significant effect of species on leaf nitrogen content (F=102.66, P<0.001; *Thalassia* > *Syringodium*; Table 4.3) and a significant effect of fertilisation (F=46.63, P<0.001; values higher follwing fertilisation; Table 4.3), but the interaction between species and fertilisation was not significant (F=1.82, P=0.19).

These results confirm that leaf nitrogen content of *Thalassia* is higher than *Syringodium* in both monospecific and mixed stands, supporting the suggestion that *Thalassia* is more

**Table 4.3.** Leaf tissue nutrient concentrations (as % DW) and daily nutrient demand (ug $g^{-1}$) for *Thalassia* and *Syringodium* in unfertilised and fertilised monospecific and mixed stands. Values are means (n=8 quadrats) ± standard errors.

| | UNFERTILISED | | | | FERTILISED | | | |
|---|---|---|---|---|---|---|---|---|
| | Monospecific | | Mixed | | Monospecific | | Mixed | |
| | Mean | ± SE | Mean | ± SE | Mean | ± SE | Mean | ± SE |
| ***Thalassia testudinum*** | | | | | | | | |
| % N | 1.84 | 0.07 | 1.85 | 0.05 | 2.76 | 0.09 | 2.26 | 0.07 |
| % P | 0.18 | 0.01 | 0.18 | 0.01 | 0.18 | 0.003 | 0.17 | 0.003 |
| N-demand | 450.58 | 47.22 | 554.65 | 77.27 | 725.32 | 47.38 | 690.38 | 79.33 |
| P-demand | 44.79 | 4.59 | 53.87 | 8.34 | 48.33 | 2.53 | 52.77 | 5.60 |
| ***Syringodium filiforme*** | | | | | | | | |
| % N | 1.33 | 0.04 | 1.40 | 0.03 | 1.94 | 0.04 | 1.68 | 0.03 |
| % P | 0.15 | 0.006 | 0.15 | 0.003 | 0.13 | 0.001 | 0.12 | 0.001 |
| N-demand | 309.33 | 37.71 | 263.61 | 39.29 | 554.40 | 28.49 | 489.75 | 37.35 |
| P-demand | 35.26 | 4.75 | 27.71 | 3.87 | 37.91 | 1.72 | 35.92 | 2.41 |

effective than *Syringodium* at obtaining sediment nutrients (see Section 4.2, Field Observation 4). The results also confirm that leaf nitrogen content increased following fertilisation in both monospecific and mixed stands of both *Thalassia* and *Syringodium*, indicating that nitrogen became more available to both species following fertilisation.

In monospecific stands, there was a significant effect of species on leaf phosphorous content (F=123.56, P<0.001; *Thalassia* > *Syringodium*; Table 4.3), a significant effect of fertilisation (F=4.02, P<0.05; values lower following fertilisation; Table 4.3) and a significant interaction effect (F=5.45, P<0.03), which indicates that the change in phosphorous content following fertilisation differed between species. The results were identical in mixed stands. There was again a significant effect of species on leaf phosphorous content (F=128.22, P<0.001; *Thalassia* > *Syringodium*; Table 4.3), a significant effect of fertilisation (F=16.10, P<0.001; values lower following fertilisation; Table 4.3) and a significant interaction effect (F=9.30, P<0.05), which indicates that the change in phosphorous content following fertilisation differed between species.

These results confirm that, as was the case for leaf nitrogen content, leaf phosphorous content of *Thalassia* is higher than *Syringodium* in both monospecific and mixed stands, supporting the suggestion that *Thalassia* is more effective than *Syringodium* at obtaining sediment nutrients. Interestingly, the results suggest that leaf phosphorous content in both monospecific and mixed stands decreased following fertilisation, but that the change differed between species. The change following fertilisation was therefore looked at separately for *Thalassia* and *Syringodium*. Leaf phosphorous content did not change following fertilisation in either monospecific or mixed stands of *Thalassia* (Table 4.3; Two-Sample t-test; monospecific: t=0.17, P=0.87; mixed: t=0.56, P=0.60). However, leaf phosphorous content decreased significantly following fertilisation in both monospecific and mixed stands of *Syringodium* (Table 4.3; monospecific: t=8.06, P<0.001; mixed: t=8.19, P<0.001).

#### 4.4.1.5 *Nutrient Demand of Thalassia and Syringodium*

In monospecific stands, there was a significant effect of species on nitrogen demand (Two-Way Analysis of Variance; F=14.53, P<0.001; *Thalassia* > *Syringodium*; Table 4.3), a significant effect of fertilisation (F=40.28, P<0.001; values higher following fertilisation; Table 4.3) and no interaction between species and fertilisation (F=0.13, P=0.72). The results were identical in mixed stands. There was a significant effect of species on nitrogen demand (F=15.90, P<0.001; *Thalassia* > *Syringodium*; Table 4.3), a significant effect of fertilisation (F=8.61, P<0.001; values higher following fertilisation; Table 4.3) and no interaction between species and fertilisation (F=0.71, P=0.41).

Nutrient demand in this study is a measure of the rate at which the plant is incorporating nutrients into plant tissue. The higher nitrogen demand observed for *Thalassia* than *Syringodium* in both monospecific and mixed stands, but particularly the fact that demand is higher in unfertilised environments (Table 4.3), is therefore consistent with the suggestion that *Thalassia* is more effective at obtaining sediment nutrients. The results do not support the contention that earlier colonisers (e.g. *Syringodium*) necessarily have higher nutrient demands than later colonisers (e.g. *Thalassia*) (see Section 4.2, Field Observation 5).

In monospecific stands, there was a significant effect of species on phosphorous demand (F=7.52, P<0.001; *Thalassia* > *Syringodium*; Table 4.3), but no effect of fertilisation (F=0.72, P=0.40) and no interaction effect (F=0.02, P=0.90). The results were identical in mixed stands. There was a significant effect of species on phosphorous demand (F=15.21, P<0.001; *Thalassia* > *Syringodium*; Table 4.3), but no effect of fertilisation (F=0.42, P=0.52) and no interaction effect (F=0.54, P=0.47).

These data on phosphorous demand, along with those on nitrogen demand, indicate that *Thalassia* displays a higher nutrient demand than *Syringodium* in St. Lawrence Bay, supporting the suggestion that *Thalassia* may be more effective than *Syringodium* at obtaining sediment nutrients. The lack of an effect of fertilisation on phosphorous demand observed in both monospecific and mixed stands is consistent with the earlier results indicating that leaf phosphorous content either did not change (*Thalassia*) or decreased (*Syringodium*) following fertilisation in this study.

## 4.4.2 Light Competition

### 4.4.2.1 *Effects of Syringodium Canopy Removal on Thalassia*

Average growth rates of *Thalassia* in the presence and absence of *Syringodium* over the 6-week period of the clipping and regrowth experiment are shown in Table 4.4. Percent differences in *Thalassia* leaf growth in the presence and absence of *Syringodium* over the 6 weeks of regrowth are shown in Figure 4.1A. In an unfertilised environment, there was a significant effect of *Syringodium* canopy removal on *Thalassia* growth rate (Two-Way Analysis of Variance: F=69.45, P<0.001), a significant effect of time on *Thalassia* growth rate (F=69.87, P<0.001), and a significant interaction effect, which suggests that the effect of *Syringodium* canopy removal on *Thalassia* growth changed over time. It is therefore useful to explore the effects of *Syringodium* canopy removal on *Thalassia* growth rate separately for each time period. Growth rate was significantly higher in the absence of *Syringodium* than in its presence for the first 3 weeks of regrowth (Two-Sample t-test; week 1: t=10.48, P<0.001; week 2: t=2.64, P<0.02; week 3: t=2.75, P<0.01).

Specific leaf productivity rates of *Thalassia* in the presence and absence of *Syringodium* over the 6-week experiment are shown in Table 4.4, and percent differences in specific leaf productivity rate are shown in Figure 4.1A. Specific leaf productivity rate was higher in the absence of *Syringodium* for the first 5 weeks of regrowth. Productivity per shoot of *Thalassia* in the presence and absence of *Syringodium* is shown in Table 4.4, and percent differences in productivity per shoot are shown in Figure 4.1A. Productivity per shoot was

**Table 4.4.** Average leaf growth rate (cm $d^{-1}$), specific leaf productivity rate (mg $g^{-1}$ $d^{-1}$) and productivity (mg $shoot^{-1}$ $d^{-1}$) for *Thalassia* in the presence and absence of a *Syringodium* leaf canopy under unfertilised and fertilised conditions. Values for growth rate are means (n=15 shoots) ± standard errors.

| | **GROWTH RATE** | | | | **SPECIFIC LEAF PRODUCTIVITY RATE** | | **PRODUCTIVITY PER SHOOT** | |
|---|---|---|---|---|---|---|---|---|
| | **Present** | | **Absent** | | **Present** | **Absent** | **Present** | **Absent** |
| | **Mean** | **± SE** | **Mean** | **± SE** | | | | |
| **Unfertilised** | | | | | | | | |
| Week 1 | 0.49 | 0.04 | 1.13 | 0.04 | 19.80 | 36.97 | 8.08 | 16.08 |
| Week 2 | 0.46 | 0.05 | 0.59 | 0.02 | 18.70 | 35.67 | 6.72 | 9.00 |
| Week 3 | 0.40 | 0.01 | 0.48 | 0.03 | 9.86 | 21.69 | 4.98 | 5.51 |
| Week 4 | 0.36 | 0.03 | 0.35 | 0.03 | 10.43 | 26.61 | 5.09 | 5.04 |
| Week 5 | 0.31 | 0.02 | 0.36 | 0.03 | 15.96 | 24.02 | 4.62 | 4.67 |
| Week 6 | 0.49 | 0.02 | 0.46 | 0.04 | 25.10 | 19.00 | 4.72 | 5.52 |
| **Fertilised** | | | | | | | | |
| Week 1 | 0.50 | 0.04 | 0.67 | 0.04 | 17.85 | 29.74 | 4.79 | 5.36 |
| Week 2 | 0.49 | 0.04 | 0.64 | 0.03 | 17.08 | 25.00 | 5.93 | 7.78 |
| Week 6 | 0.57 | 0.03 | 0.62 | 0.06 | 25.92 | 27.49 | 7.66 | 7.84 |

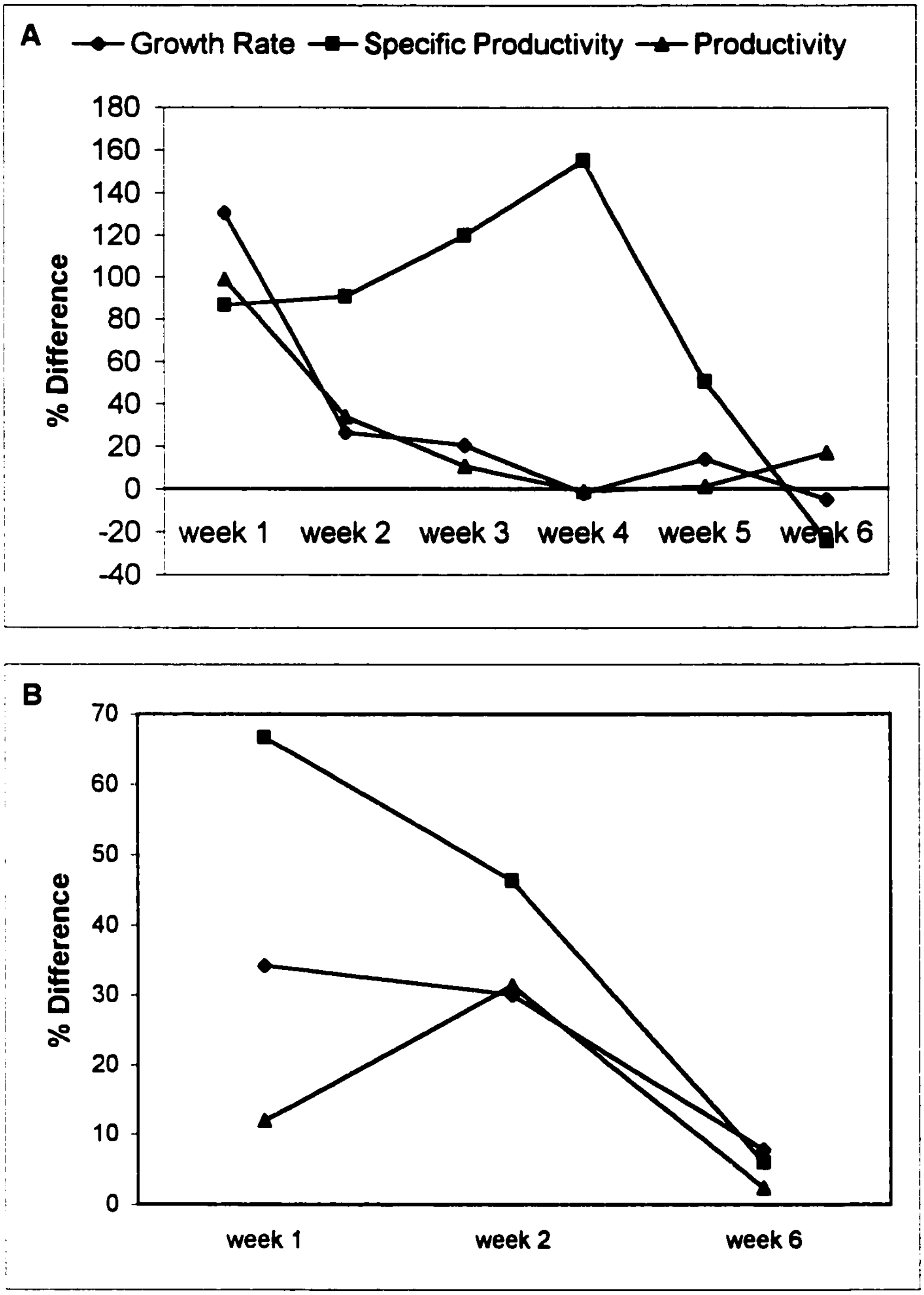


**Figure 4.1.** Percent differences in *Thalassia* growth indices in the presence and absence of a *Syringodium* leaf canopy under **(A)** Non-fertilised and **(B)** Fertilised conditions.

higher in the absence of *Syringodium* for the first 3 weeks of regrowth. These results, along with those for average growth rate, suggest that the presence of a *Syringodium* leaf canopy significantly reduces *Thalassia* leaf growth variables over at least the first 3 weeks of regrowth, after which *Thalassia* leaves may be long enough to avoid shading effects by *Syringodium*.

The *Syringodium* canopy removal experiment was repeated with fertilised plots, but regrowth was only measured at 1-week, 2-week and 6-week intervals. Average growth rates of *Thalassia* in the presence and absence of *Syringodium* are shown in Table 4.4, and percent differences in *Thalassia* leaf growth in the presence and absence of *Syringodium* are shown in Figure 4.1B. There was a significant effect of *Syringodium* canopy removal on *Thalassia* growth rate (F=13.79, P<0.001), but no effect of time on growth rate (F=0.26, P=0.77) and no interaction effect (F=1.37, P=0.26). When average growth rate was analysed separately in each time period, growth rate was significantly higher in the absence of *Syringodium* than in its presence for the first 2 weeks of regrowth (week 1: t=2.97, P<0.006; week 2: t=3.02, P<0.006).

Specific leaf productivity rates of *Thalassia* in the presence and absence of *Syringodium* are shown in Table 4.4, and percent differences are shown in Figure 4.1B. Specific leaf productivity rate was higher in the absence of *Syringodium* over the 6 weeks of regrowth. Productivity per shoot of *Thalassia* in the presence and absence of *Syringodium* is shown in Table 4.4, and percent differences in productivity per shoot are shown in Figure 4.1B. Productivity per shoot was higher in the absence of *Syringodium* over the 6 weeks of regrowth. These results are consistent with the results of the unfertilised growth experiment, and further suggest that the presence of a *Syringodium* leaf canopy significantly reduces *Thalassia* leaf growth variables following clipping and regrowth.

#### 4.4.2.2 *Effects of Thalassia Canopy Removal on Syringodium*

Average growth rates of *Syringodium* in the presence and absence of *Thalassia* over the 6-week period of the clipping and regrowth experiment are shown in Table 4.5. Percent differences in *Syringodium* leaf growth in the presence and absence of *Thalassia* over the 6 weeks of regrowth are shown in Figure 4.2A. In an unfertilised environment, a Two-Way Analysis of Variance detected no effect of *Thalassia* canopy removal on *Syringodium* growth rate (F=0.11, P=0.75), but a significant effect of time on *Syringodium* growth (F=106.49, P<0.001), and a significant interaction effect (F=2.17, P<0.05), which indicates that the effect of *Thalassia* canopy removal on *Syringodium* growth changed over time. The effects of *Thalassia* canopy removal on *Syringodium* growth rate were therefore analysed separately for each time period. Growth rate was significantly higher in the absence of *Thalassia* than in its presence for only the first week of regrowth (Two-Sample t-test; t=2.33, P<0.04).

Specific leaf productivity rates of *Syringodium* in the presence and absence of *Thalassia* over the 6-week experiment are shown in Table 4.5, and percent differences are shown in Figure 4.2A. Specific leaf productivity rates were higher in the absence of *Thalassia* for only the first week of regrowth. Productivity per shoot of *Syringodium* in the presence and absence of *Thalassia* is shown in Table 4.5, and percent differences are shown in Figure 4.2A. Productivity per shoot was higher in the absence of *Thalassia* in the first week of regrowth. These results, along with those for average growth rate, suggest that the presence of a *Thalassia* leaf canopy significantly reduces *Syringodium* leaf growth, but only for the first week of regrowth.

The *Thalassia* canopy removal experiment was repeated with fertilised plots, but re-growth was only measured at 1-week, 2-week and 6-week intervals. Average growth rates of *Syringodium* in the presence and absence of *Thalassia* in the fertilised plots are shown in Table 4.5, and percent differences are shown in Figure 4.2B. There was a significant effect of *Thalassia* canopy removal on *Syringodium* growth (F=25.37, P<0.001), a significant effect

**Table 4.5.** Average leaf growth rate (cm $d^{-1}$), specific leaf productivity rate (mg $g^{-1}$ $d^{-1}$) and productivity (mg $shoot^{-1}$ $d^{-1}$) for *Syringodium* in the presence and absence of a *Thalassia* leaf canopy under unfertilised and fertilised conditions. Values for growth rate are means (n=15 shoots) ± standard errors.

| | **GROWTH RATE** | | | | **SPECIFIC LEAF PRODUCTIVITY RATE** | | **PRODUCTIVITY PER SHOOT** | |
|---|---|---|---|---|---|---|---|---|
| | **Present** | | **Absent** | | **Present** | **Absent** | **Present** | **Absent** |
| | **Mean** | **± SE** | **Mean** | **± SE** | | | | |
| **Unfertilised** | | | | | | | | |
| Week 1 | 1.05 | 0.05 | 1.24 | 0.07 | 19.33 | 27.35 | 0.57 | 0.73 |
| Week 2 | 0.67 | 0.05 | 0.68 | 0.05 | 27.88 | 22.00 | 0.69 | 0.60 |
| Week 3 | 0.66 | 0.06 | 0.60 | 0.04 | 30.00 | 21.00 | 0.90 | 0.65 |
| Week 4 | 0.38 | 0.04 | 0.35 | 0.04 | 16.82 | 15.00 | 0.55 | 0.40 |
| Week 5 | 0.30 | 0.04 | 0.29 | 0.03 | 13.68 | 15.84 | 0.45 | 0.47 |
| Week 6 | 0.25 | 0.02 | 0.26 | 0.02 | 9.95 | 8.09 | 0.40 | 0.42 |
| **Fertilised** | | | | | | | | |
| Week 1 | 1.16 | 0.10 | 1.53 | 0.14 | 27.01 | 38.11 | 0.71 | 0.89 |
| Week 2 | 0.97 | 0.07 | 0.86 | 0.07 | 28.13 | 23.20 | 1.04 | 0.97 |
| Week 6 | 0.41 | 0.03 | 0.35 | 0.03 | 15.31 | 15.11 | 0.90 | 0.81 |

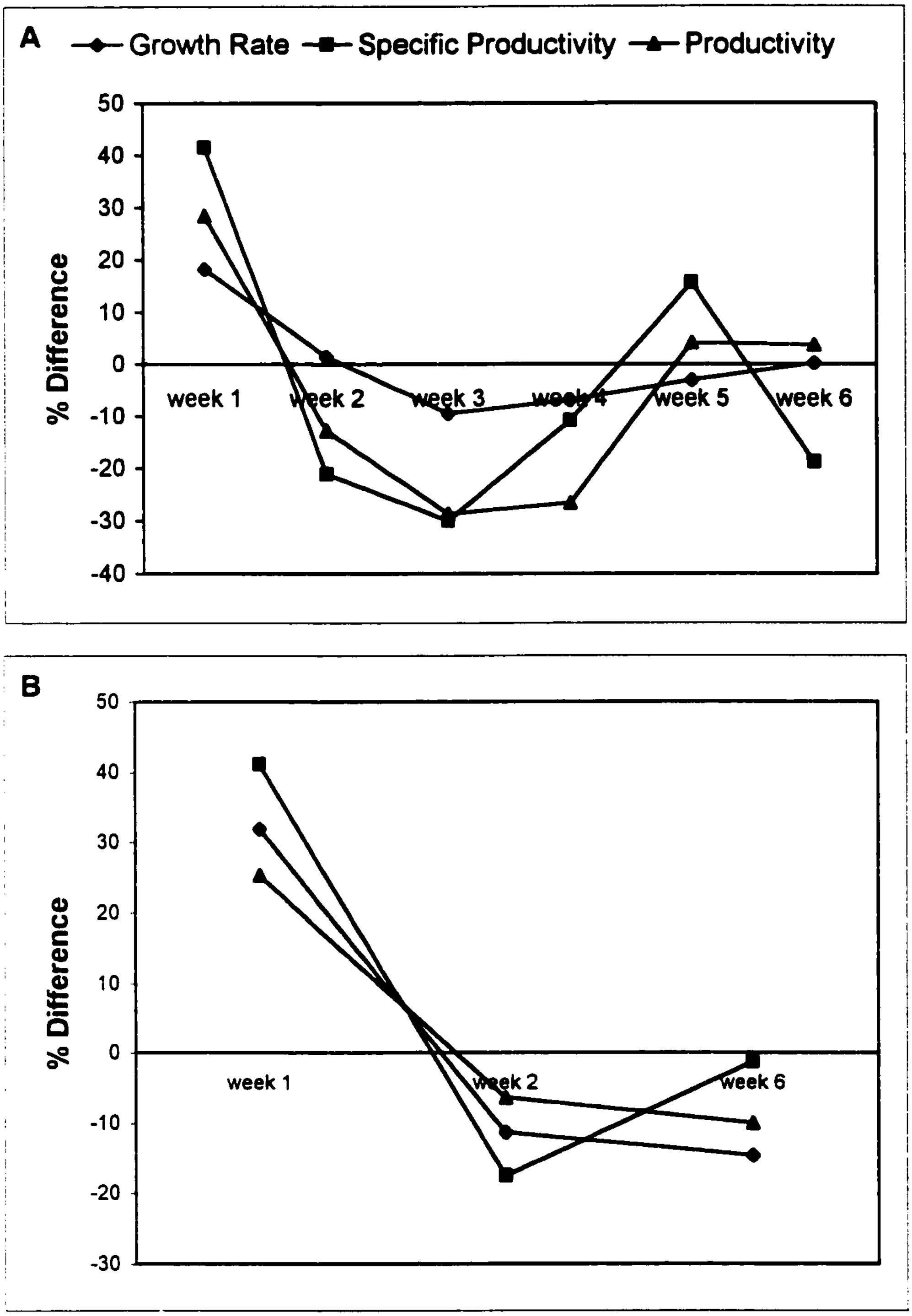


**Figure 4.2.** Percent differences in *Syringodium* growth indices in the presence and absence of a *Thalassia* leaf canopy under **(A)** Non-fertilised and **(B)** Fertilised conditions.

of time on *Syringodium* growth (F=95.36, P<0.001), and a significant interaction effect (F=15.07, P<0.001), which indicate that the effect of *Thalassia* canopy removal on *Syringodium* growth rate changes over time. The effects of *Thalassia* canopy removal on *Syringodium* growth rate were therefore analysed separately for each time period. As was the case in the unfertilised experiment, growth rate was significantly higher in the absence of *Thalassia* than in its in presence for only the first week of regrowth (t=2.20, P<0.04).

Specific leaf productivity rates of *Syringodium* in the presence and absence of *Thalassia* are shown in Table 4.5, and percent differences are shown in Figure 4.2B. Specific leaf productivity rates were higher in the absence of *Thalassia* over the first week of regrowth. Productivity per shoot of *Syringodium* in the presence and absence of *Thalassia* is shown in Table 4.5, and percent differences are shown in Figure 4.2B. Productivity per shoot was higher in the absence of *Thalassia* in the first week of regrowth. These results are consistent with the results of the unfertilised growth experiment, suggesting that the presence of a *Thalassia* leaf canopy significantly reduces *Syringodium* leaf growth variables for only about 1 week following clipping and regrowth.

### 4.4.3 Allocation of Biomass to Plant Components

The ratio of belowground biomass to aboveground biomass was significantly higher in *Thalassia* than *Syringodium* in both monospecific (Two-Sample t-test: t=15.31, P<0.001) and mixed stands (t=9.28, P<0.001), the ratio being 2-3 times higher in *Thalassia* than *Syringodium* (Table 4.2). The percentage of total biomass that is root material is about 21-24 % in *Thalassia*, but only about 10 % in *Syringodium* (Table 4.2). By contrast, the percentage of total biomass that is leaf material is about 17-19% in *Syringodium*, but only about 7-9 % in *Thalassia* (Table 4.2). The results support the suggestion that *Syringodium*'s ratio may provide it with a higher capacity to obtain and utilise light per unit of biomass to support than *Thalassia*, and that this characteristic may make *Syringodium* the more effective light competitor. The results are consistent with the contention that *Thalassia* may have a higher capacity to obtain and store sediment nutrients per unit of biomass to support than *Syringodium*, and that this characteristic may make *Thalassia* the more effective nutrient competitor (see Section 4.2, Field Observation 6; also Chapter 3, this thesis).

## 4.4 DISCUSSION

The growth and abundance of *Thalassia* decreased, and the abundance of *Syringodium* increased, in response to the 15-month discharge of a nutrient rich turbid plume into St. Lawrence Bay, Barbados (Chapter 3, this thesis). It was suggested in Chapter 3 that the *Thalassia* decline resulted from reduced light following the increased turbidity; and that the *Syringodium* increase was a response to increased sediment nutrient availability resulting primarily from the *Thalassia* loss. The first suggestion requires *Syringodium* to function more effectively than *Thalassia* under conditions of reduced light, since *Syringodium* abundance increased under the light conditions suggested to have suppressed *Thalassia*. The second suggestion requires that *Thalassia* can inhibit *Syringodium* through competition for sediment nutrients, perhaps implying that *Thalassia* is the more effective competitor. The results of the present Chapter strongly suggest that *Syringodium* is a more effective light competitor than *Thalassia* and that *Thalassia* is a more effective sediment nutrient competitor than *Syringodium*. The results therefore support the explanations provided for the changes in *Thalassia* and *Syringodium* in response to the discharge event described in Chapter 3.

Several of the results emerging from the Nutrient Experiment, and from the complementary measurements of seagrass biomass and growth, support the suggestion that *Thalassia* is a more effective competitor than *Syringodium* for sediment nutrients. In the Nutrient Experiment, *Syringodium* showed a greater growth response following fertilisation than did *Thalassia*, suggesting that *Syringodium* growth is more suppressed than *Thalassia* growth by limited nutrient availability, and hence that *Thalassia* is more effective than *Syringodium* at using limited sediment nutrients.

The typical leaf nitrogen content (as % DW N) of *Thalassia* in non-fertilised stands in this study was about 1.85 %, and the typical leaf nitrogen content of *Syringodium* was about 1.33 to 1.40 %. The typical leaf phosphorous content of *Thalassia* was about 0.18 %, and that of *Syringodium* about 0.15 %. Two points should be noted from these values. The first is that the values are at or less than those suggested by Duarte (1990) as indicative of the point at which seagrasses can be considered nutrient-limited (1.8 % N, 0.2 % P), which supports the contention that seagrasses in St. Lawrence Bay are primarily nutrient-limited. The second is that the values for *Thalassia* are significantly higher than those for *Syringodium*, supporting the suggestion that *Thalassia* has the better capacity to obtain sediment nutrients when the latter are limiting (see Section 4.2; Field Observation 4). This suggestion is further supported by the observation that the total biomass per m$^2$ of *Thalassia* in monospecific stands was significantly higher than that of *Syringodium* in monospecific stands in this study. Given that the St. Lawrence Bay environment is considered to be nutrient-limited (see above), the greater biomass per m$^2$ of *Thalassia* suggests that it is more effective than *Syringodium* at obtaining sediment nutrients (see Section 4.2; Field Observation 1).

Leaf biomass per shoot, leaf productivity per shoot and specific leaf productivity rate were compared in monospecific and mixed stands of *Thalassia* and *Syringodium* in the study. The rationale was that, for *Thalassia*, the variables should be lower in monospecific than mixed stands, since nutrient competition should be more extreme for *Thalassia* in the former; and that, for *Syringodium*, the variables should be lower in mixed stands than in monospecific stands, since nutrient competition for *Syringodium* should be more extreme in the former (see Section 4.2; Field Observations 2 and 3). For *Thalassia*, leaf biomass per shoot, leaf productivity per shoot and specific leaf productivity rate were higher in mixed than monospecific stands. These results provide further support for the suggestion that *Thalassia* is more effective at obtaining sediment nutrients, and hence of suppressing growth of nutrient competitors, than is *Syringodium*. For *Syringodium*, productivity per shoot and specific leaf productivity rate tended to be lower in mixed than in monospecific stands in an unfertilised environment, but the differences were not statistically significant and disappeared following fertilisation. This is weak support for the suggestion that nutrient competition for *Syringodium* should be more extreme in mixed than monospecific stands. Leaf biomass per shoot of *Syringodium* did not differ significantly between stand types. The inability to detect a difference in *Syringodium* leaf biomass per shoot between mixed and monospecific stands may partly reflect a limited capacity of the parameter to vary (number of leaves per shoot is typically 2 in *Syringodium*), and a limited capacity to measure changes that may occur (leaf width and hence leaf biomass is small in *Syringodium*; changes are difficult to measure).

In the Light Experiment, *Syringodium* growth responded positively to *Thalassia* canopy removal, and *Thalassia* growth responded positively to *Syringodium* canopy removal, confirming that light competition between *Syringodium* and *Thalassia* occurs in St. Lawrence Bay. The Light Experiment was conducted at deeper sites (1.2 m) than the sites used for the Nutrient Experiment and the supporting field measurements on nutrient competition (0.6-0.8 m). The fact that both light competition and nutrient competition can be detected in St. Lawrence Bay supports recent suggestions (e.g. Agawin *et al.* 1996; Terrados *et al.* 1999) that seagrass systems may often be close to both nutrient and light limitation thresholds, and that one can move from nutrient limitation to light limitation over small spatial scales.

*Syringodium* leaf growth, specific leaf productivity rate and productivity per shoot were all higher following the removal of the *Thalassia* leaf canopy in both fertilised and unfertilised experiments, but only for 1 week of regrowth. This suggests that *Thalassia* can inhibit *Syringodium* growth through light competition, but that the effect is short-lived. Williams (1987) also reported a positive *Syringodium* response following *Thalassia* canopy removal, although the effect was more detectable as shoot density than growth changes. *Thalassia* leaf growth, specific leaf productivity rate and productivity per shoot were all higher following the removal of the *Syringodium* leaf canopy in both the fertilised and unfertilised experiments, and the effect was detectable for at least 3 weeks following regrowth. The results suggest that *Syringodium* can inhibit *Thalassia* growth through light competition to a greater extent than *Thalassia* can inhibit *Syringodium* growth, supporting the suggestion that *Syringodium* is the more effective light competitor.

It is of interest to note that *Syringodium*'s growth in the absence of *Thalassia* exceeds its growth in the presence of *Thalassia* for only 1 week of regrowth. Thereafter, growth tends either not to differ in the presence or absence of *Thalassia*, or to be slightly lower in *Thalassia*'s absence. Since *Syringodium*'s growth variables were measured as total regrowth following clipping, this may reflect a higher breakage rate of *Syringodium* leaves in the absence of *Thalassia* than in its presence. Williams (1987) has previously suggested that the *Thalassia* leaf canopy can reduce breakage of *Syringodium* leaves.

The results presented in this Chapter supporting the suggestion that *Thalassia* is the more effective competitor for sediment nutrients and *Syringodium* the more effective competitor for light, are relevant not only to the interpretation of the changes in *Thalassia* and *Syringodium* observed in response to the discharge event described in Chapter 3, but also to the more general issue of the sequence and reversal of seagrass colonisation in the Caribbean. The results clearly support the contention that later colonisers (e.g. *Thalassia*) suppress earlier colonisers (e.g. *Syringodium*) because they are more effective competitors for sediment nutrients (e.g. Williams 1987, 1990). The results also support the suggestion that eutrophication will reverse the seral development of seagrass colonisation (Powell *et al.* 1991; Lapointe *et al.* 1994; Fourqurean *et al.* 1995). The reduced water clarity that may accompany eutrophication will inhibit the later coloniser (*Thalassia*) more than the earlier coloniser (*Syringodium*), since the latter are more effective at utilising light; and the increased nutrient availability will permit abundance increases in the earlier colonisers (see also Fourqurean *et al.* 1995 for the suggestion that the earlier coloniser *Halodule* is a better light competitor than *Thalassia*).

Other results emerging from this study are relevant to perspectives on seagrass colonisation. It is typically suggested that early colonisers precede later colonisers in early succession because they can generate new plant biomass faster and can therefore colonise open spaces more rapidly (e.g. Gallegos *et al.* 1994; Fourqurean *et al.* 1995). Specific leaf productivity rates of *Syringodium*, the earlier coloniser, and *Thalassia*, the later coloniser, differed little in this study, and similarity in growth indices of *Syringodium* and *Thalassia* has been reported in previous studies (Williams and McRoy 1977, 1982; Zieman *et al.* 1989). It is important to note that growth rate will be important in predicting early successional sequence when colonisation is by vegetative propagation of adjacent open spaces, i.e. when colonisation is essentially an expansion of an existing bed. However, colonisation of open spaces distant from existing beds must occur by sexual reproduction and dispersal. Differences in the rates of seed dispersal through differences in sexual reproduction rates may therefore strongly influence the early successional sequence, some colonisers typically preceding others in the successional sequence primarily because they reach distant spaces sooner. It is relevant in this context that *Syringodium* has a substantially higher rate of sexual reproduction than *Thalassia* (Gallegos *et al.* 1992, 1994).

Recent studies indicate that earlier colonisers in marine plant communities have higher nutrient demands than later colonisers (Fourqurean *et al.* 1995; Pedersen and Borum 1997), and Fourqurean *et al.* (1992, 1995) suggest that this characteristic explains their subsequent suppression in the successional sequence. The rationale is that, if earlier colonisers have higher nutrient demands, declining sediment nutrient availability as succession proceeds will result in their suppression, since their higher demands cannot be satisfied. Nutrient demand is typically measured as specific leaf productivity rate x the concentration of nutrients in leaf tissue, i.e. it is a measure of the rate at which the plant is incorporating nutrients into leaf tissue (Fourqurean *et al.* 1992). In this study, both nitrogen and phosphorous demand, measured as above, were greater in *Thalassia* (the later coloniser), than *Syringodium* (the earlier coloniser). This contradicts the contention that earlier colonisers have higher nutrient demands (see Section 4.2; Field Observation 5).

There are several reasons why nutrient demand, measured as indicated above, will be a poor indicator of which species is more likely to be suppressed as succession proceeds and available sediment nutrients decrease. The first is that the rate at which the plant is incorporating nutrients into plant tissue at any given time says little about its minimum nutrient requirements, and hence about its capacity to retain biomass as sediment nutrients decline. The value obtained for nutrient demand at a given measurement time is unlikely to be a fixed species-specific characteristic, but will vary with prevailing environmental conditions. For example, in a nutrient-limited environment, the species that will show the higher rate of incorporation of nutrients into plant tissue will be the species which is more effective at removing nutrients from the sediments (see nutrient demand of *Thalassia* and *Syringodium* in this study). The species measured as having the higher nutrient demand will therefore not be the less effective nutrient competitor, but the more effective nutrient competitor.

The second reason why nutrient demand, measured as specific leaf productivity rate x leaf nutrient concentration, will poorly predict which species prevails as sediment nutrients decline, is that this measure will seriously underestimate the total nutrient demand of species with high ratios of belowground biomass to aboveground biomass. In an interspecies comparison, a species identified as having the lower nutrient demand through use of its rate of nutrient incorporation in leaf tissue, may actually have the higher total nutrient demand, if its aboveground to belowground biomass ratio is low.

The third reason for concern with the use of nutrient demand for predicting successional sequence is that, even if the demand being realised at any moment in time were an accurate reflection of the plant's minimum nutrient requirements, it still might not predict the response of the plant to declining sediment nutrients. The important question may not be which species has the higher nutrient requirement, *sensu* must incorporate more nutrients in order to retain a unit of plant biomass, for seagrass species may not differ substantially in this context. The more important questions may be, which species has the higher capacity to obtain and store sediment nutrients per unit of biomass to support, and what characteristics would provide this capacity. It is the capacity to obtain and store more sediment nutrients per unit of biomass to support that should best predict which species suppressses which as succession proceeds and sediment nutrients decline.

A potential morphological index of the capacity to obtain and store sediment nutrients per unit of biomass to support is the ratio of belowground to aboveground biomass, and more specifically, the percentage of total biomass that is root material (see Section 4.2; Field Observation 6). In this study, the ratio of belowground to aboveground biomass was 2-3 times higher in *Thalassia* than *Syringodium* and the percentage of total biomass that is root material was about 21-24 % in *Thalassia*, but only about 10 % in *Syringodium*. Williams (1987, 1990), Powell *et al.* (1989) and Short *et al.* (1993) have previously provided data which support the contention that *Thalassia* has a substantially higher belowground to aboveground biomass ratio than *Syringodium*. These morphological characteristics may provide *Thalassia* with a greater capacity than *Syringodium* to obtain and store sediment nutrients per unit of biomass to support, and may therefore underlie the observation that *Thalassia* is the more effective nutrient competitor, suppressing *Syringodium* as succession proceeds and sediment nutrient availability decreases. As the necessary converse of this, *Syringodium* has a substantially higher aboveground to belowground biomass ratio, with the percentage of total biomass that is leaf material being about 17-19 % in *Syringodium* but only about 7-9 % in *Thalassia* in this study. This characteristic should provide *Syringodium* with a greater capacity than *Thalassia* to obtain light per unit of biomass to support, and may explain why *Syringodium* is a more effective competitor for light than *Thalassia*. There are at least two further characteristics of *Syringodium* that could contribute to its being the more effective light competitor. The first is that *Syringodium* leaves are more buoyant than *Thalassia* leaves. *Syringodium* leaves therefore float more vertically in the water column than *Thalassia* leaves, which may ensure that they more effectively interfere with *Thalassia*'s access to incident light from the water surface than *Thalassia* interferes with *Syringodium*. The second characteristic is the cylindrical shape of *Syringodium* leaves compared to the strap shaped leaves of *Thalassia*. This may ensure that *Syringodium* can more effectively absorb light through the leaf surface than *Thalassia* regardless to the angle at which the leaf lies in relation to the direction of incident light at the leaf surface.

Further consideration should be given to the changes in leaf nutrient content that occurred following fertilisation in the present study. Leaf nitrogen content increased significantly following fertilisation of monospecific and mixed stands of both *Thalassia* and *Syringodium*. By contrast, leaf phosphorous content did not change following fertilisation of either monospecific or mixed stands of *Thalassia*, and leaf phosphorous content was significantly lower following fertilisation of both monospecific and mixed stands of *Syringodium*. Despite the increase in leaf nitrogen content, neither productivity per shoot nor specific leaf productivity rate increased in *Thalassia* following fertilisation. By contrast, *Syringodium* productivity per shoot and specific leaf productivity rate increased in both monospecific and mixed stands following fertilisation. The *Thalassia* results support the suggestion in Chapter 1 that *Thalassia* in Barbados may now be primarily phosphorous-limited. The *Syringodium* results suggest that *Syringodium* in St. Lawrence Bay is nitrogen-limited, since a significant growth response to nitrogen enrichment was observed. It is of interest to note that the leaf nitrogen content of *Thalassia* prior to fertilisation was about 1.85 %, i.e. marginally over the value suggested by Duarte (1990) to indicate nitrogen limitation, and *Thalassia* did not respond to nitrogen enrichment in this study. By contrast, the leaf nitrogen content of *Syringodium* was about 1.33 to 1.40 %, i.e. well below the value suggested by Duarte (1990) to indicate nitrogen limitation, and *Syringodium* showed a strong response to the nitrogen enrichment. Agawin *et al.* (1996) and Terrados *et al.* (1999) have emphasised that the nature and extent of nutrient limitation can vary between seagrass species in the same environment, and can vary within species over relatively small spatial scales.

The lack of increase in leaf phosphorous content following fertilisation in this study is difficult to explain. One possibility is that the phosphorous did not adequately release from the fertiliser stakes. This problem was experienced by Kenworthy and Fonseca (1992) in nutrient addition experiments with slow-release fertilisers on *Zostera marina* and *Halodule wrightii*. A second possibility is that the phosphorous released from the fertiliser stakes, but that the high adsorptive capacity of the relatively fine-grained carbonate sediments characteristic of the study site (see Patriquin 1972 for sediment size characteristics of the study site; see Kitano *et al.* 1978 and Erftemeijer and Middelburg 1993 for verification of high adsorptive capacity of this sediment type) ensured that phosphorous availability to the seagrass plants did not increase. A third possibility, which could be applicable to the *Syringodium* results, is that the phosphorous was released and became more available to the *Syringodium* plants, but that its increased use by *Syringodium* leaves, as a consequence of the positive growth response of *Syringodium*, surpassed the increased phosphorous supply rate, thereby ensuring no change in phosphorous concentration in the leaf tissues. The observation that leaf nutrient content can decrease in more temperate seagrasses during summer growth peaks, because nutrient supply rate does not match leaf demand (e.g. Pedersen and Borum 1993; Perez-Llorens and Niell 1993), supports the suggestion that nutrient leaf concentration need not increase in response to nutrient enrichment, providing that there is a positive growth response such that the increased nutrient use matches the increased rate of supply. Despite this possibility, the suggestion that the phosphorous did not become more available to the seagrass plants following the fertilisation event is considered the better explanation for the leaf phosphorous results obtained in this study. Two sets of observations support this conclusion. The first is that *Thalassia* showed no growth response to the nutrient enrichment, but *Thalassia* leaf phosphorous did not change following fertilisation. If the phosphorous had become more available, the *Thalassia* leaf phosphorous levels should have increased. The second is that *Syringodium* leaf phosphorous decreased significantly following fertilisation. This suggests that the increased demand for phosphorous resulting from the positive growth response of *Syringodium* was not matched by an increase in phosphorous supply, implying that phosphorous availability did not increase following fertilisation. It is important to note that, if *Thalassia* in St. Lawrence Bay is now primarily phosphorous-limited and *Syringodium* primarily nitrogen-limited, and if phosphrous did not release in the fertiliser experiment, this alone could explain the greater growth response of *Syringodium* than *Thalassia* during the Nutrient Experiment; i.e. the difference in response need not imply that *Thalassia* was suppressing *Syringodium* more than the reverse through nutrient competition.

A general point on competitive ability of seagrass species emerges from the present results. It is reasonable to expect that both light availability and sediment nutrient availability will decrease as seagrass succession proceeds and total seagrass biomass increases (Williams

1987, 1990 ). Ideally, later colonisers should therefore be better competitors for both nutrients and light. Several results presented in this Chapter suggest that the later coloniser *Thalassia* is the more effective sediment nutrient competitor, and there is a clear indication that the earlier coloniser *Syringodium* is the more effective competitor for light. It seems likely that this difference results from a necessary trade-off in intra-plant biomass allocation, and hence in morphological design. The very characteristic which may make *Thalassia* the more effective sediment nutrient competitor (i.e. a high belowground to aboveground biomass ratio, and particularly a high ratio of root biomass to total biomass) may ensure that it is the less effective light competitor, by ensuring a low aboveground to belowground biomass ratio, and particularly a low ratio of leaf biomass to total biomass. Tilman's (1985, 1987, 1988) resource ratio hypothesis emphasises that characteristics which allow a species to be an effective competitor for one category of limiting resource are likely to constrain its effectiveness as a competitor for a second category of limiting resource, and hence that competitive superiority is likely to reverse among species, depending on prevailing environmental conditions. The results of the present study indicating that *Thalassia* is the more effective sediment nuutrient competitor and *Syringodium* the more effective light competitor, are consistent with this hypothesis. The results are less supportive of Grime (1984), who contends that certain species are superior competitors to others in all circumstances, but that the abundance of inferior competitors may increase relative to better competitors through their greater tolerance to environmental stress.

It is often emphasised (e.g. Williams 1987; Powell *et al.* 1991) that seagrass succession in the Caribbean is typically not characterised by the replacement of early colonisers by later colonisers, but rather by a change in their relative abundance. Coexistence is a common feature of Caribbean seagrass communities. The coexistence of *Syringodium* and *Thalassia* is typically ascribed to some partitioning of the sediment nutrient resource resulting from interspecific differences in mean root depth. The present results suggest that coexistence may also be facilitated by differences in competitive abilities of *Thalassia* and *Syringodium* for different categories of limiting resource. Specifically, the fact that *Thalassia* may be the more effective sediment nutrient competitor and *Syringodium* the more effective light competitor will facilitate coexistence, particularly in situations where the nature and extent of the limiting resource varies over small spatial scales.

# CHAPTER 5 CHANGES IN ABUNDANCE AND LEAF GROWTH OF SEAGRASSES IN THE EASTERN CARIBBEAN: 1969-1994

## 5.1 ABSTRACT

Changes in abundance and leaf growth of *Thalassia testudinum*, and in abundance of *Syringodium filiforme*, at several locations around Carriacou and at 2 sites (Bath, St. Lawrence) in Barbados, were assessed over the 25-year period 1969-1994. Seagrass sites originally sampled in 1969 were revisited in 1994, and the same growth and abundance variables measured. The variables were frequency of occurrence, maximum leaf length, leaf width, shoot density and leaf biomass for *Thalassia*, and frequency of occurrence and leaf biomass for *Syringodium*. At Carriacou, none of the changes in abundance and growth of *Thalassia* or *Syringodium* between 1969 and 1994 were statistically significant; but all values for *Thalassia* either decreased or remained the same, and the abundance variables for *Syringodium* increased. Total seagrass abundance at Carriacou did not change. At St. Lawrence and Bath, all *Thalassia* growth and abundance variables were significantly lower in 1994 than 1969, and the abundance of *Syringodium* was higher. Total seagrass abundance at St. Lawrence did not change between 1969 and but decreased appreciably between 1969 and 1994 at Bath. It is suggested that the impact of Hurricane Allen in 1980 is the biggest contributor to the decrease in *Thalassia* abundance observed at the Barbados sites, and that the increase in *Syringodium* is a response to increased sediment nutrient availability following the *Thalassia* loss. Sand accretion at St. Lawrence may have contributed to the decrease in *Thalassia* abundance, and through this, to the increase in *Syringodium* abundance at that site. Possible causes of the decrease in *Thalassia* growth at Bath and St. Lawrence include the increase in *Syringodium* abundance, since light competition between *Syringodium* and *Thalassia* occurs in Barbados and *Syringodium* is the more effective light competitor; a long-term decrease in coastal water quality in Barbados, although quantitative data do not exist to confirm this trend; and a shift to a younger shoot age distribution of *Thalassia* following the

impact of Hurricane Allen, but it is uncertain whether this effect could be retained for long enough to explain the lower growth rate observed almost 15 years after the hurricane event.

## 5.2 INTRODUCTION

Seagrass beds are productive coastal habitats, important in the conservation of coastal biodiversity (e.g. Zieman 1983; Hatcher *et al.* 1989; Fonseca and Cahalan 1992; Tomascik *et al.* 1997). Their nearshore location makes them vulnerable to anthropogenic coastal impacts and Hemminga (1995) has suggested that more than 65 % of documented declines in seagrass populations are attributable to human activities. Poor water quality, specifically turbidity and eutrophication, is a frequently reported cause of seagrass decline (Fonseca *et al.* 1998; Livingston *et al.* 1998; Chapter 3, this thesis), but other common anthropogenic impacts include physical damage by dredging, anchors and propellors (Taylor and Saloman 1968; Dawes *et al.* 1997), industrial pollution (Cambridge and McComb 1984), and sedimentation and sediment accretion (Williams 1990; Woodward-Clyde 1998), which may be natural or may result from human modification of nearshore sediment regimes. Many natural factors are known to contribute to seagrass decline, including disease (den Hartog and Polderman 1975; Vergeer and den Hartog 1994), storm events (Poiner *et al.* 1989; Preen *et al.* 1995), and overgrazing (Valentine and Heck 1991). The cumulative consequence of the anthropogenic and natural impacts is that declines in seagrass abundance have been reported over a wide geographical scale (e.g. Florida: Fourqurean and Robblee 1999; Hall *et al.* 1999; Zieman *et al.* 1999; Australia: Cambridge *et al.* 1986; Walker and McComb 1992; Netherlands: den Hartog and Polderman 1975; Mediterranean: Marba *et al.* 1996).

In the Caribbean, *Thalassia testudinum* is the climax species in seagrass bed development. The general successional sequence is colonisation of substrata by rhizophytic green macroalgae, followed by the seagrasses *Halodule wrightii* and/or *Syringodium filiforme*, and ending with *T. testudinum* (den Hartog 1971; Zieman 1976; Williams 1987, 1990). Mature seagrass stands (i.e. 95% substratum cover) dominated by *Thalassia* take between 15 and 50 years to develop (Patriquin 1975; Duarte 1995), and the predominance of *Thalassia* in the Caribbean may therefore be indicative of a system which has remained relatively undisturbed for an extended period. However, there is a qualitative perception of seagrass decline in many

Caribbean countries, and the substantial seagrass losses that have occurred in Florida Bay are now well documented (Fourqurean and Robblee 1999; Hall *et al.* 1999; Zieman *et al.* 1999).

Little information exists on seagrass growth and abundance in the eastern Caribbean, defined here as Barbados and the islands in the Lesser Antilles chain. The principal published studies are those of Patriquin (1971, 1972, 1973, 1975). Patriquin's work was conducted in 1969 at two sites (Bath, St. Lawrence) in Barbados, and at several locations around Carriacou. At these 3 sites, he documented several abundance and growth variables for the dominant seagrass *Thalassia testudinum*. These included an index of seagrass area coverage, shoot density, leaf biomass, maximum leaf length, leaf width, number of leaves per shoot, leaf productivity and leaf growth rate.

The principal objective of this Chapter is to take advantage of the historical data set created by Patriquin's work to assess long-term changes in growth and abundance of seagrasses in the eastern Caribbean. The same seagrass sites surveyed by Patriquin were revisited in 1994, and the same growth and abundance variables remeasured. This comparison, supplemented by an analysis of aerial photographs, allowed seagrass changes which have occurred over the 25-year period 1969 to 1994 to be documented. The study sites differ in their exposure to anthropogenic and natural disturbances, and therefore provide the opportunity to comment on long-term changes detected in this context. This 25-year comparison is one of only a few studies anywhere that have assessed seagrass changes over an extended time period (but see Birch and Birch 1984 in Australia; Fletcher and Fletcher 1995 in Central Florida; Fourqurean and Robblee 1999, Hall *et al.* 1999, and Zieman *et al.* 1999 in Florida Bay; and note the recent establishment of a monitoring program on selected seagrass variables in Barbados by the Caribbean Coastal Marine Productivity Program (CARICOMP); Parker and Oxenford 1998).

## 5.3 METHODS

### 5.3.1 Field Measurements in 1969

Aerial photographs and groundtruthing were used by Patriquin in 1969 (see Patriquin 1971) to map the extent and locations of seagrass beds, and of different substrate types within the beds, at Bath and St. Lawrence in Barbados, and at Carriacou in the Grenadine island chain (see Figure 5.1 for site locations in the eastern Caribbean). During groundtruthing at each of Bath and St. Lawrence, an onshore-offshore transect was sited such that it could be relocated on subsequent sampling occasions, and additional onshore-offshore transects (7 at Bath; 5 at St. Lawrence) were sited at specific distances away from and parallel to the reference transect. The principal function of the transects was to obtain onshore-offshore depth data, and to allow for relocation of sites. Twelve 10 m x 10 m stations were then selected at Bath, 26 at St. Lawrence and 23 at Carriacou. The locations of the stations at Bath and Carriacou were chosen to be representative of the range of environmental conditions impacting on the seagrass beds at the sites (e.g. depth, wave action, substrate type; this was particularly necessary for Carriacou for depth and wave action, and Bath for substrate type). Selection of sites at St. Lawrence was random across the seagrass beds, since conditions were more homogeneous at St. Lawrence.

At each 10 m x 10 m station, the presence or absence of seagrass species was documented within 12 randomly placed 50 cm x 50 cm (0.25 $m^2$) quadrats. Seagrass abundance and growth variables were measured in 3 randomly placed 25 cm x 25 cm (0.0625 $m^2$) quadrats which were then used to collect data on seagrass abundance and growth variables within each station. To do this, all seagrass within each of the 0.0625 $m^2$ quadrats was harvested to substrate level, and maximum leaf length, leaf width, shoot density and leaf biomass were recorded in the laboratory for the climax seagrass species *Thalassia testudinum*. Maximum leaf length was the average of the 10 longest leaves from the 3 quadrats, except when there were less than a total of 200 leaves, in which case maximum leaf length was the average of

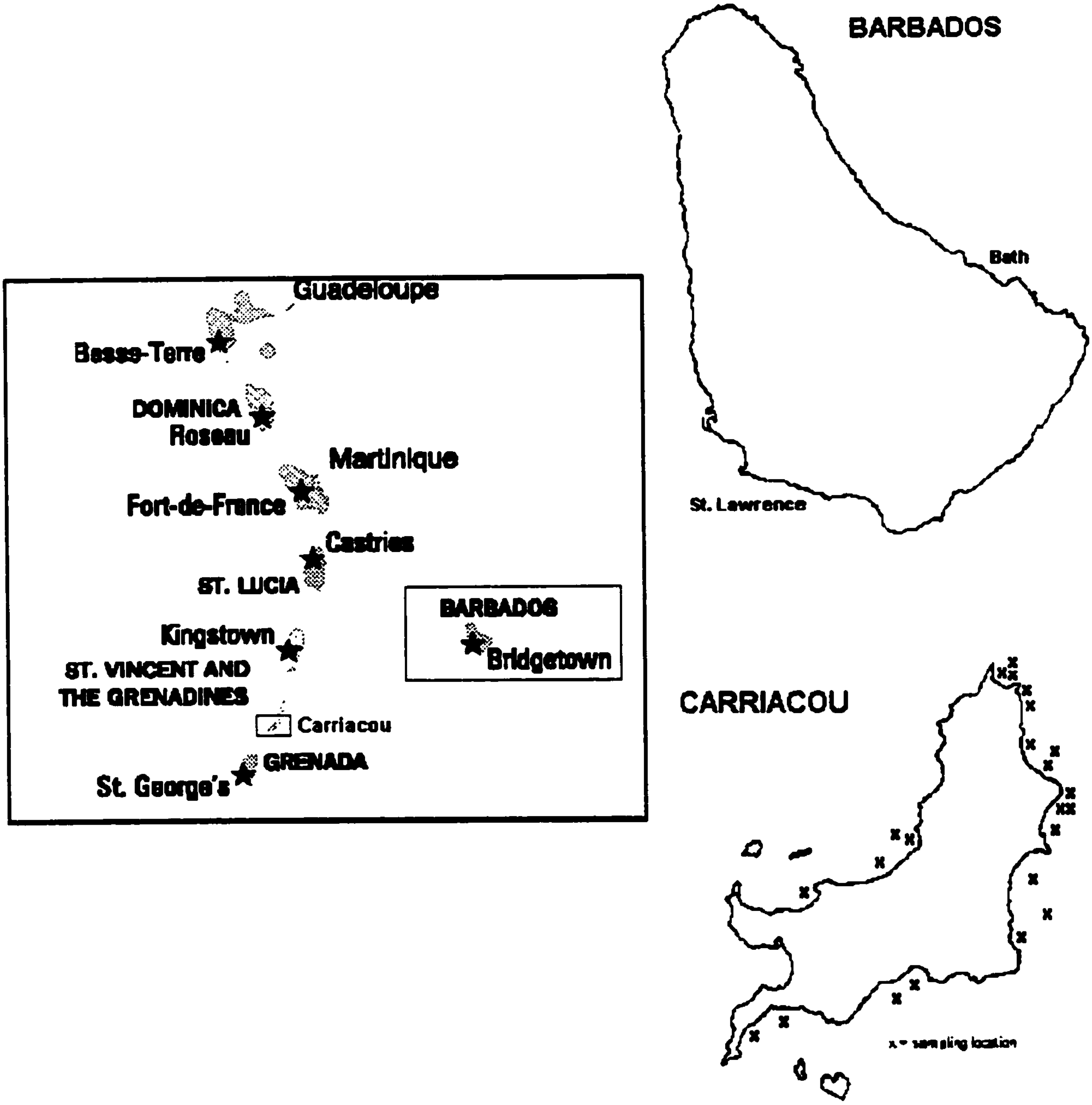


Figure 5.1. Location of study sites in the eastern Caribbean.

the longest 5 % of the leaves (Appendix B). Leaf width was obtained by randomly selecting and measuring the widths of 35 leaves from the quadrats. Shoot density was not measured directly, but was estimated as described in Appendix B. Leaf biomass was measured as the wet weight of leaves per $m^2$ in the quadrats. Leaf biomass was also measured at the 3 sites for *Syringodium filiforme*, as described for *Thalassia* above. The 1969 data were collected between December 1969 and April 1969. Details of the data collection methodology for the 1969 data set are provided in Appendix B.

### 5.3.2 Field Measurements in 1994

The 3 study sites (Bath, St. Lawrence, Carriacou) were revisited in 1994, and the sample stations used in 1969 were relocated at each site. At Bath and St. Lawrence, the stations were relocated using the transect lines established in 1969. At Carriacou, the stations were relocated using aerial photographs and depth data collected in 1969. At Bath and Carriacou, all of the relocated stations still had seagrass; at St. Lawrence, 4 of the 26 stations did not. The abundance variables at the St. Lawrence site were calculated both including and excluding sample stations which did not contain seagrass in 1994. The former approach is taken as producing a minimum abundance estimate and the latter a maximum abundance estimate for St. Lawrence in 1994. The same seagrass growth and abundance variables measured for each station in 1969 were measured in 1994. However, the number of 25 cm x 25 cm quadrats used to collect data in each station was increased from 3 to 5 quadrats for Bath, and from 3 to 6 quadrats for St. Lawrence, to compensate for the absence of seagrass in some quadrats at these two sites in 1994. The 1994 growth and abundance data at each station were collected between February 1994 and April 1994 by a team of field scientists, the senior members of which were D. Patriquin, R. Scheibling and L. Vermeer.

### 5.3.3 Data Analysis

Data were tested for normality and homogeneity of variance, and transformed when necessary to satisfy assumptions of parametric statistics. Frequency of occurrence data were arcsine square root transformed, and the remaining abundance variables were natural log (x+1) transformed since some of the values were zero due to the absence of seagrass in some quadrats in 1994. All growth variables were natural log transformed. Differences in abundance and growth variables at each of the 3 study sites between 1969 and 1994 were analysed using paired-sample t-tests, paired by sample station.

### 5.3.4 Aerial Photographs

Aerial photographs were used to quantify changes in the distribution and abundance (area covered) of seagrasses at Bath and St. Lawrence over a 27-year period. Specifically, the aerial photographs used were sets for Bath and St. Lawrence taken in 1964 by Hunting Surveys Ltd., in 1983 by Procter and Redfern International Ltd., and in 1991 by Terra Surveys. Interpretation of the aerial photographs in terms of the extent and distribution of seagrass beds was facilitated by groundtruthing exercises conducted at Bath and St. Lawrence in 1969, 1986 and 1994. Groundtruthing in 1986 was conducted by C. Parker as a component of a study of sea urchin habitat in Barbados.

Using the information gathered from groundtruthing, the distribution and extent of seagrass beds at the study sites was identified on the aerial photographs. The seagrass beds were digitised with reference to the Barbados National Grid. The digitised beds were then incorporated into a GIS system which was used to produce maps showing the distribution and cover of the seagrass beds at the study sites in each year, and to calculate changes in the area of seagrass coverage between years.

### 5.3.5 Study Sites

Carriacou is an undeveloped and relatively pristine island with a total area of 34 km$^2$, and a population of about 5,000. Population density is therefore only about 147 per km$^2$. This contrasts with a current population density of about 613 per km$^2$ in Barbados, and suggests that seagrass beds in Carriacou may in general be less impacted by anthropogenic activities than seagrass beds in Barbados. The locations of the survey stations in Carriacou were distributed islandwide to facilitate a representative sampling of the seagrass communities (Figure 5.1). The substrate of the seagrass stands sampled is predominantly sand, with a limited occurrence of cobble sand and cobble framework substrates. The mean low water depth of the stands varied between 0.5 and 9 m. The most extensive seagrass beds in Carriacou occur in shelf lagoons on the east (windward) coast, and are afforded protection by offshore barrier reefs. As is the case for the east coast of Barbados, wave action on the east coast of Carriacou is strong and often subject to strong tidal currents. Seagrass beds also occur on the leeward coast, but are not as extensive as those on the windward coast. A general descritpion of the ecological and oceanographic characteristics of the seagrass beds around Carriacou is provided by Patriquin (1971).

The St. Lawrence and Bath study sites are described in Chapter 1, Section 1.3.1 of this thesis.

## 5.4 RESULTS AND DISCUSSION

### 5.4.1 Differences in abundance and growth between 1969 and 1994 at the 3 Study Sites

#### 5.4.1.1 *Carriacou*

The mean values for the abundance and growth variables at the Carriacou study site in 1969 and 1994 are shown in Table 5.1. None of the changes in abundance and growth between 1969 and 1994 were statistically significant ($P>0.05$). However, all values for *Thalassia* either decreased or remained the same, with the decrease in maximum leaf length and in leaf biomass approaching statistical significance (Table 5.1). By contrast, the abundance variables for *Syringodium* were higher in 1994 than in 1969, with the change in leaf biomass of *Syringodium* approaching statistical significance (Table 5.1). Total seagrass leaf biomass at the Carriacou study site did not change between 1969 and 1994 (Table 5.1).

#### 5.4.1.2 *St. Lawrence*

The mean values for the abundance and growth variables at the St. Lawrence study site in 1969 and 1994 are shown in Table 5.2. All of the *Thalassia* abundance and growth variables were significantly lower in 1994 than in 1969 (but note that the decrease in frequency of occurrence was not significant if maximum abundance estimates for 1994 are used); the decrease in the remaining variable (leaf width) approached statistical significance (Table 5.2). These results strongly suggest that both growth (as indicated by maximum leaf length and leaf width, and abundance (as indicated by frequency of occurrence, shoot density and leaf biomass) of *Thalassia*, were lower in 1994 than in 1969. By contrast, frequency of occurrence and leaf biomass of *Syringodium* were higher in 1994 than in 1969, the increase being statistically significant if maximum abundance estimates for 1994 are used (Table 5.2).

**Table 5.1.** Abundance and growth variables for the seagrasses ***Thalassia testudinum*** and *Syringodium filiforme* at the Carriacou site in 1969 and 1994. All values are means of 23 stations. Frequency of occurrence at a station is the % occurrence in 12 quadrats at the station. P-values indicate the results of comparisons between 1969 and 1994 using Paired-sample t-tests (paired by station). Standard errors (SE) are provided.

| | **1969** | | **1994** | | | |
|---|---|---|---|---|---|---|
| **VARIABLE** | **Mean** | **SE** | **Mean** | **SE** | **% change** | **P-value** |
| **Frequency of Occurrence of *Thalassia*** | 100.0 | 0 | 98.6 | 1.1 | -1.4 | 0.18 |
| ***Thalassia* Shoot Density (shoots $m^{-2}$)** | 401.0 | 47.9 | 355.2 | 51.5 | -11.4 | 0.43 |
| ***Thalassia* Leaf Biomass (wet weight g $m^{-2}$)** | 729.8 | 99.7 | 609.6 | 93.8 | -16.5 | 0.1 |
| ***Thalassia* Maximum Leaf Length (cm)** | 22.7 | 0.9 | 20.8 | 1.0 | -8.4 | 0.07 |
| ***Thalassia* Leaf Width (mm)** | 9.6 | 0.2 | 9.6 | 0.3 | 0 | 0.87 |
| **Frequency of Occurrence of *Syringodium*** | 47.8 | 10.6 | 53.6 | 10.2 | 12.1 | 0.59 |
| ***Syringodium* Leaf Biomass (wet weight g $m^{-2}$)** | 234.6 | 58.8 | 344.1 | 90.8 | 46.7 | 0.06 |
| **Total Seagrass Leaf Biomass (wet weight g $m^{-2}$)** | 964.4 | 77.2 | 964.9 | 95.9 | 0.0 | 0.99 |

be retained some 15 years following the hurricane event, are unclear. A second possibility is that it results from reduced water clarity, since *Thalassia* was shown to be sensitive to reduced light in this study, but long-term data on coastal water clarity in Barbados are not available. Finally, the increased *Syringodium* abundance could in principle be contributing to the decreased *Thalassia* growth, since light competition between *Thalassia* and *Syringodium* was demonstrated in this study, and *Syringodium* was shown to be the more effective light competitor.

**Table 5.2.** Abundance and growth variables for the seagrasses *Thalassia testudinum* and *Syringodium filiforme* at the St. Lawrence site in 1969 and 1994. Frequency of occurrence, shoot density and leaf biomass are presented as minimum and maximum (*) values; minimum values include stations with no seagrass in 1994 and are therefore means of all 26 stations, and maximum values exclude the 4 stations without seagrass in 1994 and are therefore means of 22 stations. For leaf length and leaf width, values are means of 18 stations. Frequence of occurrence at a station is the % occurrence in 12 12 quadrats at the station. P-values indicate the results of comparisons between 1969 and 1994 using Paired-sample t-tests (paired by station). Total seagrass area was determined from aerial photographs taken in 1964 and 1991. Standard errors (SE) are provided where possible.

| | **1969** | | **1994/95** | | | |
|---|---|---|---|---|---|---|
| **VARIABLE** | **Mean** | **SE** | **Mean** | **SE** | **% change** | **P-value** |
| **Frequency of Occurrence of *Thalassia*** | 85.6 | 5.7 | 66.7 | 7.8 | -22.0 | 0.02 |
| | 91.3* | 4.7 | 78.9* | 6.3 | -13.6 | 0.12 |
| ***Thalassia* Shoot Density (shoots $m^{-2}$)** | 333.9 | 45.8 | 189.2 | 34.5 | -43.3 | 0.007 |
| | 368.8* | 50.0 | 223.6* | 36.2 | -39.3 | 0.02 |
| ***Thalassia* Leaf Biomass (wet weight g $m^{-2}$)** | 606.9 | 85.8 | 281.0 | 4.8 | -53.7 | 0.001 |
| | 664.1* | 95.1 | 332.1* | 49.5 | -50.0 | 0.003 |
| ***Thalassia* Maximum Leaf Length (cm)** | 21.9 | 0.6 | 18.9 | 0.6 | -13.5 | 0.01 |
| ***Thalassia* Leaf Width (mm)** | 10.6 | 0.2 | 9.9 | 0.2 | -6.6 | 0.12 |
| **Frequency of Occurrence of *Syringodium*** | 65.1 | 8.7 | 82.6 | 7.2 | 27.0 | 0.19 |
| | 58.7* | 9.7 | 97.7* | 1.7 | 66.4 | 0.0006 |
| ***Syringodium* Leaf Biomass (wet weight g $m^{-2}$)** | 536.8 | 101.6 | 751.8 | 147.8 | 40.0 | 0.28 |
| | 491.5* | 114.4 | 888.4* | 157.9 | 80.9 | 0.07 |
| **Total Seagrass Leaf Biomass (wet weight g $m^{-2}$)** | 1143.7 | 68.5 | 1032.9 | 167.4 | -9.7 | 0.56 |
| | 1155.5* | 72.3 | 1220.7* | 168.9 | 5.6 | 0.74 |

| | **1964** | **1991** | **% change** |
|---|---|---|---|
| **Total Seagrass Area ($m^2$)** | 18068 | 19939 | 10.4 |

Total seagrass leaf biomass at the St. Lawrence study site did not differ significantly between 1969 and 1994 (Table 5.2). Moreover, total area of seagrass did not differ appreciably, being bigger by only 10% (Table 5.2).

### 5.4.1.3 *Bath*

The mean values for the abundance and growth variables at the Bath study site in 1969 and 1994 are shown in Table 5.3. All of the *Thalassia* abundance and growth variables were signficantly lower in 1994 than in 1969 (Table 5.3). By contrast, frequency of occurrence and leaf biomass of *Syringodium* was substantially higher in 1994 than in 1969 (% increase 71.4 and 84.2 respectively), but the increase was not statistically significant for either variable (Table 5.3). Total seagrass leaf biomass decreased by 54% between 1969 and 1994, but the increase was again not statistically significant (Table 5.3). Consistent with the decrease in total leaf biomass, the total area covered by seagrass decreased by about 42% between 1969 and 1994 (Table 5.3). These results strongly suggest that both growth and abundance of *Thalassia* were substantially lower in 1994 than in 1969 at the Bath study site. The decreases in both abundance and growth variables appear to be greater at the Bath site than at the St. Lawrence site (compare Tables 5.2 and 5.3).

## 5.4.2 Causes of Abundance and Growth Changes

The results of this study suggest that both the abundance and growth variables of *Thalassia* were significantly lower in 1994 than in 1969 at the Bath and St. Lawrence sites in Barbados, but that the abundance of *Syringodium* at the 2 sites was higher in 1994 than in 1969. Total seagrass area and abundance was substantially lower at Bath in 1994 than in 1969, but differed little at St. Lawrence. Changes in total seagrass area and total seagrass abundance are not necessarily expected when abundance trends in the 2 principal species are

**Table 5.3.** Abundance and growth variables for the seagrasses *Thalassia testudinum* and *Syringodium filiforme* at the Bath site in 1969 and 1994. Values are means of 12 stations. Frequency of occurrence at a station is the % occurrence in 12 quadrats at the station. P-values indicate the results of comparisons between 1969 and 1994 using Paired-sample t-tests (paired by station). Total seagrass area was determined from aerial photographs taken in 1964 and 1991. Standard errors (SE) are provided where possible.

| | **1969** | | **1994/95** | | | |
|---|---|---|---|---|---|---|
| VARIABLE | **Mean** | **SE** | **Mean** | **SE** | **% change** | **P-value** |
| **Frequency of Occurrence of *Thalassia*** | 100.0 | 0.0 | 75.7 | 8.5 | -24.3 | 0.003 |
| ***Thalassia* Shoot Density (shoots m$^{-2}$)** | 631.5 | 91.6 | 181.7 | 30.1 | -71.2 | 0.0001 |
| ***Thalassia* Leaf Biomass (wet weight g m$^{-2}$)** | 524.1 | 85.6 | 91.7 | 14.2 | -82.5 | 0.0007 |
| ***Thalassia* Maximum Leaf Length (cm)** | 18.9 | 1.7 | 13.6 | 0.9 | -28.1 | 0.02 |
| ***Thalassia* Leaf Width (mm)** | 9.6 | 0.5 | 8.4 | 0.3 | -12.8 | 0.02 |
| **Frequency of Occurrence of *Syringodium*** | 19.4 | 11.1 | 33.3 | 12.2 | 71.4 | 0.46 |
| ***Syringodium* Leaf Biomass (wet weight g m$^{-2}$)** | 109.4 | 73.8 | 201.5 | 108.5 | 84.2 | 0.49 |
| **Total Seagrass Leaf Biomass (wet weight g m$^{-2}$)** | 635.8 | 96.8 | 293.2 | 112.1 | -53.9 | 0.02 |
| | **1964** | | **1991** | | **% change** | |
| **Total Seagrass Area (m$^{2}$)** | 75185 | | 43998 | | -41.5 | |

in opposite directions. Growth and abundance of *Thalassia* changed much less between 1969 and 1994 at Carriacou than at St. Lawrence and Bath. Possible causes of the decreases in *Thalassia* abundance and growth, and the increase in *Syringodium* abundance, at the Barbados sites are considered below.

### 5.4.2.1 *Hurricane Impacts and Changes in Seagrass Age Structure*

A possible cause of the changes in seagrass abundance observed is the occurrence of episodic, intense storm and hurricane events. Hurricane activity can cause extensive damage to seagrass beds through wave action and/or sand abrasion, and through sand burial which results in physical smothering of plants. The wave action and sand abrasion can destroy aboveground seagrass biomass and whole plants (Birch and Birch 1984; Poiner *et al.* 1989; Meeder *et al.* 1994; van Tussenbroek 1994). Recovery of severely damaged areas can take many years (Patriquin 1975; Zieman 1976; Duarte 1995), with denuded areas persisting for extended periods in the form of "blowouts" (*sensu* Patriquin 1975), that can enlarge and migrate through the seagrass bed.

One way to assess whether hurricane impacts might be a principal cause of the changes in *Thalassia* abundance observed in this study would be to consider whether hurricane activity was more severe or more frequent at Barbados than at Carriacou, and whether it was more frequent or more severe in Barbados in the period between 1969 and 1994, when abundance of *Thalassia* was observed to have decreased, than in typical periods. The frequency, severity and proximity of hurricanes and tropical storms in the vicinity of Barbados and Carriacou in the 25-year, 10-year, and 5-year periods before 1969 and before 1994 are shown in Table 5.4. Hurricane activity has been greater at Barbados than at Carriacou, reflecting the fact that Carriacou lies to the south of Barbados, and the typical path of hurricanes through the area is north of Barbados. The greater loss in *T. testudinum* abundance at the Barbados sites than at Carriacou is therefore generally consistent with the hypothesis that the loss could result

**Table 5.4.** The frequency, severity and proximity of hurricanes and storms near Barbados and Carriacou in the 25-year, 10-year, and 5-year periods before 1994 and 1969. Hurricanes closer than 250 km, and storms closer than 100 km from land are included in the analysis. Names of hurricanes and storms are provided. Hurricanes are categorised on a scale of increasing severity from 1 to 5 based on wind speeds. Storms have been assigned a cateogry value of 0.5. Proximity of hurricanes and storms is categorised as: 1 - <50km; 2 - 50-100km; 3 - 100-150km; 4 - 150-200km; 5 - 200-250km.

| YEAR | NAME | 25-YEAR PERIOD: 1969-1993 | | | |
|---|---|---|---|---|---|
| | | BARBADOS | | CARRIACOU | |
| | | Category | Distance | Category | Distance |
| 1990 | Arthur | 0.5 | 2 | 0.5 | 2 |
| 1989 | Hugo | 4 | 5 | | |
| **5-year Cumulative (1989-1993)** | | | | | |
| 1988 | Joan | | | 0.5 | 2 |
| 1987 | Emily | 0.5 | 2 | 0.5 | 2 |
| 1986 | Danielle | 0.5 | 2 | 0.5 | 1 |
| **10-year Cumulative (1984-1993)** | | | | | |
| 1980 | Allen | 3 | 1 | 3 | 5 |
| 1979 | Ana | 0.5 | 1 | 4 | 5 |
| 1979 | David | 4 | 3 | | |
| 1978 | Cora | 0.5 | 2 | 0.5 | 2 |
| 1974 | Gertrude | 0.5 | 1 | 0.5 | 1 |
| 1970 | Dorothy | 0.5 | 2 | | |
| **25-year Cumulative (1969-1993)** | | | | | |

| YEAR | NAME | 25-YEAR PERIOD: 1944-1968 | | | |
|---|---|---|---|---|---|
| | | BARBADOS | | CARRIACOU | |
| | | Category | Distance | Category | Distance |
| 1966 | Judith | 0.5 | 1 | | |
| **5-year Cumulative (1964-1968)** | | | | | |
| 1963 | Edith | 2 | 1 | 1 | 5 |
| 1963 | Flora | 3 | 3 | 3 | 3 |
| 1961 | Anna | 0.5 | 2 | 0.5 | 2 |
| **10-year Cumulative (1959-1968)** | | | | | |
| 1956 | Betsy | 3 | 4 | | |
| 1955 | Janet | 3 | 1 | 3 | 1 |
| 1954 | Hazel | 0.5 | 2 | 1 | 2 |
| 1951 | Dog | 1 | 2 | 1 | 4 |
| 1949 | Storm #3 | 0.5 | 1 | | |
| 1945 | Storm #3 | 0.5 | 2 | | |
| 1944 | Storm #2 | 0.5 | 2 | 0.5 | 1 |
| 1944 | Storm #4 | 0.5 | 1 | 0.5 | 2 |
| **25-year Cumulative (1944-1968)** | | | | | |

from the impacts of hurricanes.

The hypothesis is less well supported by a comparison of general hurricane activity at Barbados in the period between 1969 and 1994, with that prior to 1969. The data do not suggest that 1969 to 1994 was a period of atypically high hurricane activity. However, two points require comment. First, *Thalassia* abundance may have also decreased in the period leading up to 1969, but data are not available to test this. Second, the issue may not be general hurricane activity near Barbados, but whether or not there was a direct hurricane hit. Even with direct hits of hurricanes of similar severity, impacts on coastal and marine communities can vary. A direct hit by a Category 3 hurricane did occur in Barbados between 1969 and 1994, specifically by Hurricane Allen in 1980. Mah (1984) documented considerable damage to nearshore coral reef communities in Barbados as a consequence of Hurricane Allen's impact. Aerial photographs taken in 1983, and analysed as a part of this study, indicate that the total area of seagrass at St. Lawrence and Bath in that year was 10,120 $m^2$ and 27,850 $m^2$ respectively. This is substantially lower than the area of seagrass estimated for St. Lawrence and Bath in either 1964 or 1991 (compare the 1983 estimates to those in Tables 5.2 and 5.3). This strongly suggests that the impact of Hurricane Allen in 1980 may have contributed substantially to the lower *Thalassia* abundance at Bath and St. Lawrence in 1994 compared to 1969. Patriquin *et al.* (in prep) provided topographical data for the Bath site in 1969 and 1994 which supports the suggestion of a hurricane impact at the site. Specifically, they showed that there had been disruption of the cobble-framework substratum at Bath, and the transport of considerable quantities of coral debris towards shore. The fact that the losses in *Thalassia* abundance at Bath were greater than at St. Lawrence is supportive of the suggestion that the losses were caused by hurricane impact. Fonseca *et al.* (1998) report that reductions in seagrass abundance as a result of storm events is a positive function of how exposed to wind-generated waves the seagrass bed is prior to the storm event, and Bath is a substantially more exposed site than St. Lawrence.

The apparent increase in *Syringodium* abundance at the 2 Barbados sites between 1969 and

1994 can not be the direct consequence of hurricane impacts. The immediate impact of a hurricane would be a decrease in *Syringodium* abundance, and consistent with this, total seagrass abundance at both Bath and St. Lawrence was low in 1983 following the passage of Hurricane Allen. Birch and Birch (1984) suggest that the shallower rhizome system of *Syringodium* compared to *Thalassia* may make *Syringodium* abundance losses greater than *Thalassia* abundance losses during storm events. If the observed increase in *Syringodium* abundance between 1969 and 1994 is related to a hurricane event, it would have to be a subsequent response to the hurricane-induced reduction in *T. testudinum* abundance. This is plausible since *Syringodium* is an early coloniser in the successional sequence of seagrass bed development in which *Thalassia* is the climax community species (Patriquin 1975; Williams 1990). *Thalassia* can apparently outcompete *Syringodium* for sediment nutrients as succession proceeds and seagrass densities rise (Williams 1987; Chapter 4, this thesis). A sharp reduction in *Thalassia* abundance could therefore lead to increased sediment nutrient availability and a subsequent increase in *Syringodium* abundance, and the response of *Syringodium* abundance to increased nutrient availability can apparently be rapid (see Chapters 1 and 3, this thesis). The suggestion that the increase in *Syringodium* abundance is a consequence of the decrease in *Thalassia* abundance is supported by the fact that increases in *Syringodium* abundance were greatest at Bath where losses in *Thalassia* abundance were greatest. During the discharge event described in Chapter 3, the increase in *Syringodium* abundance is suggested to be the consequence of increased sediment nutrient availability resulting from the decrease in *Thalassia* abundance.

The changes in abundance of *Thalassia* and *Syringodium* observed at the Bath and St. Lawrence sites between 1969 and 1994 could therefore in principle result from the single hurricane event which occurred in 1980, but the decreases in growth variables of *Thalassia* between 1969 and 1994 are more difficult to explain in this context. Although damage to surviving rhizomes could conceivably constrain leaf growth and leaf dimensions following a hurricane event, it is most unlikely that this constraint could remain in effect some 14 years after the event. In Barbados, leaves are produced approximately every 15-20 days (plastochron interval), and grow and reach their maximum length in about 35 days. Indeed, rather than constraining leaf growth, Duarte *et al.* (1997) suggest that there may be enhancement of seagrass growth following disturbance events, as a consequence of the increased nutrient availability resulting from the reduced seagrass abundance.

Another way in which a single hurricane event could continue to influence *Thalassia* growth rate variables for some period after the event is through changes in the shoot age structure characteristic of the seagrass stands. Major mortality events, such as a severe hurricane impact, are likely to cause significant shifts in population demographics towards a younger age structure (see Durako 1995), and recovery to the age structure characteristic of mature stands may be slow in *Thalassia* (see Duarte 1995 for suggestion that mature *Thalassia* stands may take up to 50 years to develop). Moreover, it is possible that, following a major disturbance event, the equilibrium age structure to which a population returns differs from the equilibrium age structure that existed prior to the event. All of the *Thalassia* leaf growth variables which decreased between the 1969 and 1994 studies (maximum leaf length, leaf width, leaf growth rate) are now known to decrease with decreasing leaf age (Chapter 2, this thesis). A shift in the age structure towards younger shoots following a hurricane event could therefore result in decreases in *Thalassia* growth variables. However, mechanisms by which a shift in shoot age distribution towards younger shoots could be retained for almost 15 years following a hurricane event are unclear.

#### 5.4.2.2 *Substrate Instability*

Substrate instability constrains the colonisation and development of seagrass communities (Patriquin 1975). Destabilisation of substrate supporting seagrass, whether by natural or anthropogenic causes, can disrupt and reverse the seral development of seagrass colonisation. Specifically, *Halodule wrightii* and *Syringodium*, the early colonisers in the successional development of seagrass beds in the Caribbean, are expected to increase in abundance relative to *Thalassia* under conditions of shifting sand and sand accretion. *Halodule* and *Syringodium* are suggested to have higher rates of shoot turnover and more rapid vertical stem growth than *Thalassia*, characteristics which allow them to more readily adjust to changes in the sediment surface, and thereby decrease their susceptibility to burial under sand accretion (Williams 1990; Fourqurean *et al.* 1995; Woodward-Clyde 1998; Kenworthy and Schwarzschild 1998). Duarte *et al.* (1997) showed sharp reductions in shoot density in response to sand burial in *Thalassia hemprichii*, a closely related species to *T. testudinum*, and an initial decrease in shoot densities of the earlier colonisers *Halodule wrightii* and *Syringodium isoetifolium*, followed by a subsequent recovery.

Given the above, if sand accretion has occurred between 1969 and 1994 at St. Lawrence and Bath, this could be a cause of the changes in *Syringodium* and *Thalassia* abundance observed in this study. Sand accretion is less likely at Carriacou than it is at St. Lawrence or Bath, since the Carriacou study sites are considerably deeper and are outside the zone of greatest sediment transport. Beach width and bathymetric data collected at St. Lawrence, and reported by Delcan (1995b), indicate that, at least since 1975, St. Lawrence has been characterised by an ongoing sand accretionary trend caused by anthropogenic modification of the coastline, specifically by the construction of a series of sea groynes in the area. Estimated rates of sand accumulation in the nearshore area are high (~2,000 to 5,000 $m^3$ $yr^{-1}$). Sand accumulation could therefore conceivably explain the observed decrease in *Thalassia* abundance and increase in *Syringodium* abundance at St. Lawrence. It might also explain the observed decreases in *Thalassia* growth variables observed at the site since, if *Thalassia* has to allocate more resources to increasing vertical rhizome length to keep pace with the rising sediment surface, it may have fewer resources available for leaf growth processes. However, whether trade-offs occur between vertical rhizome growth and leaf growth in *Thalassia* is unknown. In any event, littoral changes can not account for the decrease in *Thalassia* abundance and growth and increase in *Syringodium* abundance observed at Bath. The long-term trend at Bath is modest net erosion since the 1950s, and a quantitative beach monitoring program indicates that there has been no change in beach width at Bath over at least the past

10 years (Halcrow 1998b). The seagrass changes at Bath were greater than at St. Lawrence, and clearly can not be explained by significant changes in the sediment regime at that site.

### 5.4.2.3 *Eutrophication*

Lapointe *et al.* (1994) suggested that eutrophication can cause a shift in seagrass community dominance from *Thalassia testudinum* to the earlier colonising species *Halodule wrightii* and fast growing macroalgae, and a decrease in water clarity and increase in nutrient enrichment resulted in a reversal from *Thalassia* to *Syringodium* in this study (Chapter 3). Eutrophication is the most frequently cited factor influencing the decline of seagrass beds globally. It can reduce *Thalassia* growth and abundance by decreasing water clarity, either directly or indirectly through the growth of fleshy, algal epiphytes on the *Thalassia* leaves (Cambridge *et al.* 1986; Flores-Verdugo *et al.* 1988; Tomasko and Lapointe 1991; Lapointe and Clark 1992; Hemminga 1998). Since *Syringodium* abundance is constrained by nutrient availability in the presence of the more effective nutrient competitor, *Thalassia* (Williams 1987; Chapters 3 and 4, this thesis), eutrophication could increase *Syringodium* abundance by increasing nutrient availability directly as well as indirectly by causing *Thalassia* loss.

Given the above, if nutrient discharge to the coastal zone has increased between 1969 and 1994 at St. Lawrence and Bath, this could cause the changes in *Thalassia* and *Syringodium* abundance, and perhaps *Thalassia* growth, observed in this study. In contrast to Barbados, Carriacou has undergone little change in either coastal population density or agricultural practices between 1969 and 1994. Its current population density is about 147 km$^{-2}$, compared to a Barbados current population density of about 613 km$^{-2}$), and there is virtually no agricultural activity in Carriacou. It therefore seems unlikely that there has been a substantial increase in nutrient discharge to the coastal waters around Carriacou over the 25-year period.

In Barbados, freshwater enters the coastal zone as ground water discharge and surface water. Delcan (1995a) documented a 3 to 10-fold increase in nitrate contamination of ground water and surface water in Barbados between 1977 and 1994, indicating a significant increase in nitrogen discharge to the coastal zone over that period. Mean nitrate concentration in the catchment discharging into the St. Lawrence area increased from about 2.9 mg $l^{-1}$ in 1977 to about 8.4 mg $l^{-1}$ in 1992 (a total increase of about 190 %; an annual increase of 12.7 %; Delcan 1995a); mean nitrate concentration in the Bath catchment area increased from about 3.0 mg $l^{-1}$ in 1977 to about 9.0 mg $l^{-1}$ in 1996 (a total increase of 200 %; an annual increase of 10.5 %; Halcrow 1998a). The increased ground water nitrate levels in the St. Lawrence area result primarily from increased sewage contamination, reflecting the increased tourist and resident densities near the coastal zone; the increased nitrate levels in the Bath area result from increased fertiliser use in agricultural activities in the area, as well as from sewage discharge (Halcrow 1998a).

The above data suggest substantial increases in ground water nitrate levels, but ground water undergoes significant dilution on release into the coastal zone, and dispersal would be enhanced at Bath by the strong flushing characteristics of the site. The large increases in nitrate contamination of Barbados ground water over the past 2-3 decades need not therefore have impacted seagrass communities in the coastal zone, but some effects of the increased nitrogen loading may be detectable. Specifically, there is some evidence to suggest that *Thalassia* in Barbados has shifted from being primarily nitrogen-limited (Patriquin 1972) to primarily phosphorous-limited in 1999 (Chapters 1 and 4, this thesis). Given this, and given the large increase in nitrogen loading of the coastal zone reported, eutrophication could in principle have contributed to the increased *Syringodium* abundance observed at St. Lawrence and Bath, and to the decline in *Thalassia* growth and abundance observed, given *Thalassia*'s sensitivity to reduced water clarity (Chapters 3 and 4, this thesis). However, it is important to note that leaf nitrogen and phosphorous content of seagrasses in Barbados are still at or below values suggested by Duarte (1990) to indicate nutrient limitation (see Chapter 4, this thesis). Long-term effects of eutrophication on seagrass growth and abundance are therefore likely to be negligible or small. The fact that the seagrass systems in Barbados remain primarily nutrient-limited is consistent with the limited epiphytism observed. Fleshy epiphytes on leaves were scarce or absent at all study sites in 1969, and remained scarce or absent in 1994 at Carriacou. They were observed at Bath and St. Lawrence in 1994, with the degree of epiphytism being less at Bath than at St. Lawrence. However, even at St. Lawrence, epiphyte growth was not extreme, and their presence on the *Thalassia* leaves was highly ephemeral. This makes it most unlikely that epiphytes are a significant cause of the reduced growth and abundance of *Thalassia* observed at St. Lawrence or Bath.

#### 5.4.2.4 *Summary of Potential Causes of Abundance and Growth Changes*

Several factors may have contributed to the changes in *Thalassia* growth and abundance, and in *Syringodium* abundance, reported over the 25-year period at Barbados in this study. The impact of Hurricane Allen is likely to have been the biggest contributor to the decrease in *Thalassia* abundance observed at both Bath and St. Lawrence. The increase in *Syringodium* abundance may best be explained as a consequent release from *Thalassia* nutrient competition, i.e. as a response to the decreased *Thalassia* abundance resulting from the hurricane impact. There is some evidence that nitrogen loading has driven *Thalassia* in Barbados from primarily nitrogen limitation to primarily phosphorous limitation, and eutrophication could therefore in principle have contributed to the increased *Syringodium* abundance observed in the study. However, any such effect would have to be small, since seagrasses in Barbados remain primarily nutrient-limited. Sand accretion at St. Lawrence could have contributed to the decrease in *Thalassia* abundance, and through this, to the increase in *Syringodium* abundance at that site. The decrease in *Thalassia* growth evident at both St. Lawrence and Bath is more difficult to explain. One possibility is that it results from a shift to a younger age structure following the impact of Hurricane Allen, since most *Thalassia* growth variables have been shown to decrease with decreasing shoot age in this study. However, the mechanisms by which a shift to a younger shoot age distribution could

## SUMMARY

The goal of my research was to document and interpret short-term and long-term changes in growth and abundance of seagrasses (*Thalassia testudinum*, *Syringodium filiforme*) in Barbados. The short-term changes were in response to a 15-month discharge of nutrient-rich and turbid water into St. Lawrence Bay. The long-term changes were over the 25-year period 1969-1994 at 2 sites (St. Lawrence; Bath) in Barbados and at Carriacou. To facilitate interpretation of the changes, seasonal observations of growth and abundance of *Thalassia* were made, effects of shoot age on *Thalassia* growth were investigated, and studies of nutrient and light competition between *Thalassia* and *Syringodium* were conducted.

Seasonal variation in abundance, growth, shoot recruitment and shoot mortality of *Thalassia* was surveyed for 2 years at St. Lawrence and 1 year at Bath, and seasonal variation in salinity, water temperature, rainfall, air temperature, daylength, hours of sunlight, leaf nutrient levels (as an indicator of coastal nutrient levels), and abundance of *Syringodium* (as a biotic environmental factor) were documented.

Air temperature, water temperature, salinity and daylength showed only slight seasonal variation, but there was strong seasonal variation in rainfall, with most rain occurring betwen June and November. Nutrient levels (total phosphorous, total nitrogen) in *Thalassia* leaves varied significantly, with levels being highest when rain-driven land-based discharge to the coastal zone would be highest. Plastochron interval, leaf growth rate, relative leaf growth rate and specific leaf growth rate were the growth variables showing most seasonal variation, with rates being highest when nutrient availability, as indicated by leaf nutrient levels, was highest. This suggests that seasonal variation in *Thalassia* leaf growth may be driven by seasonal variation in nutrient availability.

In months when nutrients were most limiting, as indicated by C:P and C:N ratios, N:P ratios

were highest, suggesting that phosphorous was more limiting than nitrogen. In 1969, *Thalassia* in Barbados was considered to be primarily nitrogen-limited. It is possible that heavy nitrogen loading of the coastal zone over the past 3 decades in Barbados has driven the *Thalassia* systems from primarily nitrogen limitation to primarily phosphorous limitation.

Seasonal variation in *Thalassia* shoot recruitment was bimodal, with peaks in September to November and March to April. Shoot mortality rates were highest in these periods, and monthly mortality was positively correlated with monthly recruitment. This suggests that *Thalassia* may be close to a shoot density carrying capacity, and is consistent with the observation that seasonal variation in shoot density was weak (St. Lawrence) or negligible (Bath) at the Barbados study sites.

The fact that *Thalassia* leaf growth, shoot recruitment and shoot mortality showed seasonal variation in a tropical location such as Barbados suggests that all spatial comparisons of seagrass condition, and all monitoring programs to detect long-term trends in seagrasses, must be designed to control for possible seasonal variation in the variables to be measured.

Effects of shoot age on leaf growth variables of *Thalassia* were investigated in St. Lawrence Bay. The effects were investigated separately within 3 shoot age categories, those less than 1 year old (young shoots), those between 1.8 and 2.2 years old (old shoots), and those between 4.5 and 6.1 years old (oldest shoots).

Shoot age affected all leaf growth variables investigated. Leaf width increased with shoot age in all 3 age categories, with age explaining 46% of the variance in leaf width in young shoots. Leaf growth rate increased with shoot age in young shoots, and weak positive effects were detectable in both older shoot categories. Plastochron interval and maximum leaf length increased with age for young shoots. The effects were detectable in old shoots, but not in the oldest shoot age category. Leaves per shoot increased with shoot age in both older age categories, but the amount of variance explained was low, and shoot age did not affect leaves per shoot in young shoots. Relative leaf growth was negatively correlated with age in young shoots, not correlated with age in old shoots, and positively correlated with age in the oldest shoots. For all leaf growth variables except leaves per shoot, the amount of variance in growth explained by shoot age was higher in young shoots than in older age categories.

The only prior study of shoot age on leaf growth variables was on a temperate seagrass, *Cymodocea nodosa*, where positive effects of shoot age on leaf length and leaves per shoot were detected. The results of the prior and present study suggest that shoot age effects on leaf growth variables may be common in seagrasses. Knowledge of these effects for different seagrass species in different locations will be necessary for accurate interpretation of spatial and temporal variation in seagrass growth. For example, given the considerable variation in shoot age distributions observed at St. Lawrence in this study, age effects may contribute substantially to local spatial variation in seagrass growth. Moreover, given the age effects on growth detected in this study, growth declines documented by seagrass monitoring programs may result, not only from direct effects of environmental stress on growth, but also from shifts to a younger age distribution following major disturbance events.

Effects of short-term changes in coastal water quality on seagrass abundance and growth were investigated in St. Lawrence Bay, by monitoring changes in response to sub-surface water being pumped into the Bay to drain an inland site adjacent to a mangrove swamp. The discharge lasted for 15 months, but was typically restricted to about a 4 hour period daily.

Turbidity, SPM levels, nitrate concentrations and sedimentation rates were significantly higher during discharge than before discharge at the study sites, with turbidity levels being substantially in excess of recommended thresholds for seagrasses. *Thalassia* abundance, as shoot density and biomass per substrate area, as well as the area-specific growth variable, productivity, decreased significantly during the discharge event, probably as a result of reduced exposure to appropriate light levels following the increased turbidity. Negative impacts of the plume discharge were also detected on shoot-specific *Thalassia* variables, specifically leaf biomass per shoot, leaves per shoot and leaf width. Maximum leaf length, plastochron interval, and leaf growth rate did not change significantly during the discharge event, but relative leaf growth rate and specific leaf productivity rate increased during discharge.

On the basis of responsiveness to environmental stress, ease of measurement and negligible seasonal variation (Chapter 1), shoot density and leaf width are recommended as priority variables to include in *Thalassia* monitoring programs, but it should be noted that leaf width does change significantly with leaf age (Chapter 2).

The abundance of *Syringodium* increased at most sites during the discharge event, probably as a result of increased sediment nutrient availability resulting from *Thalassia* loss. The changes observed in *Thalassia* and *Syringodium* abundance support the suggestion that eutrophication, with its associated reduction in water clarity, can reverse the seral development of seagrass colonisation from the later coloniser *Thalassia* to the earlier coloniser *Syringodium*. The changes are consistent with the suggestion that *Thalassia* is the more effective competitor for sediment nutrients and *Syringodium* the more effective competitor for light.

Light and nutrient competition between *Thalassia* and *Syringodium* was investigated in St. Lawrence Bay. Two principal experiments, the Nutrient Experiment and the Light Experiment, were conducted. In the Nutrient Experiment, nutrient levels were manipulated by fertilisation, and the growth responses of *Syringodium* and *Thalassia*, as productivity per shoot and specific leaf productivity rate, were compared. *Syringodium* showed a greater growth response to fertilisation than *Thalassia*. This suggests that *Syringodium* growth may be more suppressed than *Thalassia* growth by limited nutrient availability. It supports the suggestion that *Thalassia* is more effective than *Syringodium* at using limited sediment nutrients.

Total biomass per m$^2$ of *Thalassia* in monospecific stands in St. Lawrence Bay was significantly higher than that of *Syringodium*, and leaf nitrogen and phosphorous content was higher for *Thalassia*. These observations support the suggestion that *Thalassia* has a higher capacity than *Syringodium* to obtain sediment nutrients, and hence to support plant biomass, in a nutrient-limited environment.

Biomass per shoot, productivity per shoot and specific leaf productivity rate were higher for *Thalassia* in mixed stands than monospecific stands in St. Lawrence Bay, suggesting that nutrient competition is more extreme for *Thalassia* in the latter stands. Productivity per shoot and specific leaf productivity rate were lower for *Syringodium* in mixed than monospecific stands in unfertilised environments, suggesting that nutrient competition may be more extreme for *Syringodium* in mixed stands, but the differences between stand types were not statistically significant.

In the Light Experiment, light levels were manipulated by canopy removal, and effects of *Thalassia* canopy removal on *Syringodium* growth and of *Syringodium* canopy removal on *Thalassia* growth were assessed. The results indicate that *Syringodium* inhibits *Thalassia* growth through light competition more than *Thalassia* inhibits *Syringodium* growth, suggesting that *Syringodium* is the more effective light competitor.

Data obtained from *Thalassia* and *Syringodium* plants in St. Lawrence Bay confirm that *Thalassia* has a higher belowground to aboveground biomass ratio than *Syringodium*. This provides *Thalassia* with a potentially higher capacity to obtain and store sediment nutrients per unit of total biomass to support, and provides *Syringodium* with a potentially higher capacity to obtain light per unit of total biomass to support. This morphological difference may largely explain why *Thalassia* is the more effective nutrient competitor and *Syringodium* the more effective light competitor.

The contention that *Syringodium* is the more effective light competitor, and that *Thalassia* is the more effective nutrient competitor, strengthens the validity of the explanations provided for the seagrass changes observed in response to the discharge event that occurred in St. Lawrence Bay; i.e., *Thalassia* loss primarily occurred through reduced light, and the *Syringodium* increase primarily occurred through increased nutrient availability resulting from the *Thalassia* loss.

The results of the Nutrient and Light Experiments in St. Lawrence Bay suggest that seagrasses may be constrained by both nutrient competition and light competition in the same local area, and may move between nutrient and light limitation over relatively small spatial scales. Since *Thalassia* is the more effective nutrient competitor and *Syringodium* the more effective light competitor, such situations may largely explain the coexistence of these species commonly observed in Caribbean seagrass communities.

Changes in abundance and leaf growth of *Thalassia*, and in abundance of *Syringodium*, at several locations around Carriacou and at 2 sites (Bath, St. Lawrence) in Barbados, were assessed over the 25-year period 1969-1994. Seagrass sites originally sampled in 1969 were revisited in 1994, and the same growth and abundance variables measured. Measurements occurred in the same months in both years to control for seasonal effects on the variables, now known to occur in *Thalassia* in Barbados (Chapter 1). The variables measured were frequency of occurrence, maximum leaf length, leaf width, shoot density and leaf biomass for *Thalassia*, and frequency of occurrence and leaf biomass for *Syringodium*.

At Carriacou, none of the changes in abundance and growth of *Thalassia* or *Syringodium* between 1969 and 1994 were statistically significant; but all values for *Thalassia* either decreased or remained the same, and the abundance variables for *Syringodium* increased. Total seagrass abundance at Carriacou did not change.

At St. Lawrence, all *Thalassia* growth and abundance variables were significantly lower in 1994 than 1969, and the abundance of *Syringodium* was higher. Total seagrass abundance at St. Lawrence did not change between 1969 and 1994.

At Bath, all *Thalassia* growth and abundance variables were significantly lower in 1994 than 1969, and the abundance of *Syringodium* was higher. Total seagrass abundance at Bath decreased appreciably between 1969 and 1994.

The impact of Hurricane Allen in 1980 is proposed as the biggest contributor to the decrease in *Thalassia* abundance observed at the Barbados sites. Given the nutrient competition effects between *Thalassia* and *Syringodium* observed during the discharge event in Chapter 3, and in the competition study in Chapter 4, the increase in *Syringodium* abundance between 1969 and 1994 is suggested to be primarily a response to increased sediment nutrient availability resulting from the *Thalassia* loss. Sand accretion at St. Lawrence may also have contributed to the decrease in *Thalassia* abundance, and through this, to the increase in *Syringodium* abundance at that site.

Possible causes of the decrease in *Thalassia* growth at Bath and St. Lawrence include the increase in *Syringodium* abundance, since light competition between *Syringodium* and *Thalassia* occurs in Barbados and *Syringodium* is the more effective light competitor (Chapter 4); a long-term decrease in coastal water quality in Barbados, although quantitative data do not exist to confirm this trend; and a shift to a younger shoot age distribution following the impact of Hurricane Allen, since many growth variables are now known to decrease with decreasing shoot age in *Thalassia* (Chapter 2), but the mechanisms by which a shift to a younger age distribution could be retained some 15 years following the hurricane event are unclear.

# APPENDIX A

## The Biology of Seagrasses

Seagrasses are the only marine representatives of the Angiospermae. They belong to the order Helobiae, in two families: Potamogetonaceae and Hydrocharitaceae. As vascular flowering plants, they have the same basic structure as terrestrial plants. They produce flowers, fruits and seeds and, like terrestrial grasses, have separate roots, leaves and underground stems called rhizomes which, in seagrasses, form extensive networks below the sediment surface. Seagrasses are believed to have evolved from terrestrial plants which subsequently reinvaded the sea through a gradual, progressive acclimation to shallow fresh water, shallow brackish water and eventually full immersion in sea water (den Hartog 1970). The fossil record suggests that seagrasses originated about 100 million years ago in the ancient Tethys Sea, bounded by Africa, Gondwana and Asia. By the Eocene period, they were more widely dispersed in the Asian-Pacific and neotropics. Their present geographical distribution ranges from the Arctic to the southern tips of Africa and New Zealand.

Adaptation to a submerged marine environment required anatomical, morphological and physiological hydrophytic modifications. Important among these was the extensive rhizome network below the sediment surface, which connect the erect shoots and which, along with the extensive root system, anchor the plant to the substrate. The rhizomes often also serve as a storage area, and the roots have root hairs which facilitate sediment nutrient uptake. The leaves are strap-shaped or oval, with little or no cutinous layer. This allows some nutrient intake from the water column, but most nutrient absorption is through the root system. The leaf epidermis consists of a single chlorophyllous cell layer, below which is a thick colorless aerenchyma layer with large air canals running through the length of the leaf. The air canals continue through the rhizomes and roots and into the root hairs. The canals facilitate gaseous anchorage and provide buoyancy to the seagrass leaves. The buoyancy assists the leaves in remaining erect in the water column, and ensures that detached leaves can be transported considerable distances by water currents.

Seagrasses have high light requirements and are commonly found in shallow coastal marine areas, salt marshes and estuaries, forming extensive meadows in sandy or silty sediments. They thrive best in shallow water, but can grow at depths of 32 m and have been found in clear water at a depth of 68 m. Seagrasses reproduce vegetatively and sexually by flowering. Seagrasses have separate male and female flowers, which are typically small and inconspicuous, since there is no need to attract insects for pollination. Pollen, containing the male gamete, is carried by water currents, and is often released in strands. The pollen cells are often long and thread-like, rather than small and round as in terrestrial plants. Successful fertilisation produces tiny seeds which develop inside small fruits and which are dispersed by water currents and in the faeces of herbivores. Although flowering does occur, primarily in winter and early spring, it is not a common event, and most reproduction in seagrasses is through vegetative reproduction by the growth and branching of rhizomes.

Vegetative growth involves horizontal rhizome extension from an apical meristem and vertical rhizome production of erect shoots at regular intervals behind the apex. Lateral branching of the vertical rhizome to produce new rhizome pieces occurs infrequently. The rhizomes tend to grow downward in response to eroding substratum; upward growth and branching by the vertical rhizomes occurs in response to increased siltation (Tomlinson and Vargo 1966). The rhizomes are able to translocate photosynthates between adjacent vertical shoots (ramets) (Tomasko and Dawes 1989). This has important implications for seagrasses growing in heterogeneous environments since physiological integration of shoots facilitates stress reduction on individual shoots subject to limiting conditions (Salzman and Parker 1985; Tomasko and Dawes 1989). Roots and erect short shoots arise from nodes, joint-like swellings at regular intervals along the rhizome (i.e. both horizontal and vertical), and are separated by a number of rhizome internodes. Vertical internodes represent the number of leaves produced on a shoot and are identifiable by scars left on the rhizome after leaf abscission. Leaves are produced from the erect short shoots on alternating sides of a central meristem, with new leaf growth arising from the basal meristem. Hence, tissue nearest the leaf base is the youngest portion of the leaf. Short shoots typically support between 2 to 5 leaves at a time, but this varies with seagrass species.

# APPENDIX B

## Detailed Methodology for the 1969-1994 Seagrass Comparisons (Chapter 5)

The 1994 work was sponsored by the Canadian International Development Agency (CIDA) and through the Marine Resource and Environmental Management Program (MAREMP) of the University of the West Indies. The project involved comparisons of topography, seagrasses and corals in seagrass beds of the eastern Caribbean between 1969 and 1994. The seagrass comparison was a component of the Ph.D. field research of L. Vermeer at Dalhousie University. The 1969 work was undertaken by D.G. Patriquin as a component of his Ph.D. research at Bellairs Research Institute of McGill University. The participants were [1]D.G. Patriquin[1], R.S. Scheibling[1], L. Vermeer[1,2], W. Hunte[2] and G. Patriquin[3].

### Topography and Selection of Sampling Stations

*Bath*

The extent, topography, and distribution of substrate types and seagrass species were mapped in 1969 using aerial photographs (Hunting Surveys Ltd., taken in 1964) and ground truthing. The latter was conducted by measuring depths, and observing bottom types, seagrass species and other variables along transects traversing the beds from shore to at least the seaward margin of the seagrass beds.

A reference transect was sited using onshore and offshore points that were permanent and could be relocated. Seven other transects were sited at 40 m intervals parallel to the reference transect. Consistency of direction and lateral location were maintained by lining up two target posts on shore. Distances and depths were measured using a graduated 2 m pole. The

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locations of the transects were superimposed on outlines of the seagrass beds taken from the aerial photographs and traced on plastic drafting paper. These were used in the field to confirm or adjust boundaries of the beds, and to locate further transects, observation points and sampling stations. Depths, substrate types and visibly prominent epiflora and fauna were recorded typically at 2 m intervals along the transects. Water height at a reference site was monitored at approximately 1/2 hour intervals during field work, and were adjusted to MLW using Barbados Port Authority Tide Tables for 1969.

The Bath site is highly heterogeneous. Sixteen "stations" of 10 x 10 m were selected to represent 5 different bottom types, and major differences in epibenthic flora and faunal diversity within each type. In 1994, the end points of the 1969 reference transect were relocated, and the transect observations were repeated. The transect lines were used to relocate the 1969 sampling stations, and observations were repeated at the 16 stations as in 1969.

### *St. Lawrence*

The largest of several small discrete seagrass beds at St. Lawrence was mapped in 1969 following a procedure similar to that for Bath, i.e. using aerial photographs (Hunting Surveys Ltd., taken in 1964). The reference transect ran from a sluice gate on shore to a prominent point on the reef seaward of the seagrass bed. Five other transects began at the same point as the reference transect, but were oriented at different angles. The locations of these transects were superimposed on images of the seagrass beds taken from aerial photographs on plastic drafting paper. These maps were used in the field to confirm or adjust boundaries of the beds, and to locate further transects, observation points and sampling stations.

Twenty-six 10 m x10 m stations within the seagrass bed were selected in 1969 using random numbers on a grid of 10 m x 10 m squares which covered the entire surveyed area. However, sites were selected only within the contiguous seagrass bed. In 1994, the 26 stations were located in relation to the reference transect, and the observations were repeated.

### *Carriacou*

Areas of seagrass beds were identified in 1969 from aerial photographs (United Kingdom, Directorate of Overseas Surveys, Contract 85, taken in 1966). Approximate depths were indicated by Admiralty Chart 2872, and 24 positions for establishing 10 m x10 m sampling stations were selected such that seagrass beds from various depths and degrees of exposure to wave action were represented.

At 11 sites, transects across part or all of the beds were made by swimming perpendicular to shore, maintaining the direction by reference to a wrist compass. Distances and depths were measured with a calibrated 2 m pole, or a calibrated depth gauge for depths over 2 m. The presence of different species of seagrass and corals were noted at 10 m or shorter intervals.

Twenty-four 10 m x 10 m stations were selected around the island. The particular stations were chosen by placing points on aerial photographs to provide coverage roughly proportional to the total area occupied by seagrass beds.

The transect and station observations were repeated in 1994.

## Sampling of Stations

At each station, a 10 m x 10 m plot was established, and 12 sampling points on a 10 m x 10 m grid were selected by use of random numbers. At each point, presence or absence of epibenthic faunal and floral species were observed within a 0.25 $m^2$ quadrat. Only the seagrass data are reported in this thesis. Seagrass was further sampled by throwing a 0.0625 $m^2$ quadrat into the area and collecting seagrass within the quadrat after shearing it to substrate level. Three such samples were taken at each station in 1969. In 1994, 3 samples were taken at Carriacou, but at Barbados the number was increased to compensate for the presence of bare patches; samples were taken from every second quadrat up to number 10 at

Bath (5 potential samples) and up to number 12 at St. Lawrence (6 potential samples).

The seagrass was bagged, subsequently shaken to remove free water, and then weighed fresh. These weights include water, seagrass blades and attached epiphytes. Widths of 35 blades, selected randomly, were measured to the nearest 0.5 mm, and lengths of the longest-appearing 15 blades were measured to the nearest millimeter. The parameter used to indicate leaf length in 1969 was L10 , the average length of the longest 10 leaves in the 3 samples. In the 1969 study, a highly significant, linear relationship was found between L5%, the average length of the longest 5% of the leaves, and average growth rate (Patriquin 1973). This suggested that variation in values for the L10 statistic between sites would be indicative of variation in growth rates between sites. However, the L10 statistic was not weighted by leaf density, as was L5%. For the 13 stands that were included in the growth rate studies, leaf number per three 0.0625 $m^2$ quadrats varied from 75 to 413 leaves, and the ratio of L10 to L5% from 0.94 to 1.06. This variation is very low compared to variation in growth rate (approximately 5 fold). Patriquin (1973) therefore suggested that there would be little error in using L10 as a measure of relative growth rate. However, at very low leaf densities, some weighting would obviously be necessary.

In 1994, the number of leaves in samples were counted so that a properly weighted maximum leaf length statistic could be calculated. To calculate such a statistic for the 1969 data, counts of leaves in the samples would be needed, but these had not been obtained. However, we hypothesised that the average fresh weight per leaf in a sample would be correlated with average width x L5%. This was tested on the 1994 data, and data from 11 of the stands included in the growth rate studies of 1969. For the Bath, St. Lawrence and Carriacou data, sets, $r^2$ values were 0.70, 0.45 and 0.64 respectively. For no intercept models, the slopes relating g $leaf^1$ and L5% (cm) were 0.0172, 0.0256 and 0.0293 respectively. These relationships were therefore used to estimate leaf number for the 1969 samples from data on fresh weight for whole samples, L10 and average width. For samples with low leaf numbers, the calculation was run iteratively (calculating new values for L5%, and substituting those in the equation for estimating leaf number) until the estimated L5% value did not change (two significant digits).

It should be noted that in 1969, at least 15 of the longest appearing leaves were selected for measurement, so that the longest 10 leaves would necessarily be included. We were therefore able to estimate L5% for samples of 200 and fewer leaves from the 1969 data, but not for larger samples. To avoid introducing a consistent bias in the comparisons between years, L10 is used as the measure of maximum length (Lm) for samples of 200 leaves or greater, and L5% is used for samples of less than 200 leaves, in both data sets.

In 1994, additional data were taken to estimate *Thalassia testudinum* shoot density. Counts were made of the number of *T. testudinum* leaves per shoot for each of 25 shoots sampled throughout a station, except at the St. Lawrence bed. At that site, a single statistic for the number of leaves per shoot was calculated from counts for 25 shoots sampled over the entire bed. For the 1994 data, estimates of shoot density were made by dividing the average number of leaves per shoot (measured *in situ*) into the total number of leaves per unit area (estimated from the number of leaves in the biomass samples). For the 1969 data, estimates of shoot density used the 1994 data on average number of leaves per shoot for each site, and the leaf number calculated as described above.

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