

Phosphorus Availability and Salinity Control Productivity and Demography of the Seagrass *Thalassia testudinum* in Florida Bay

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Abstract Biomass, net primary productivity (NPP), foliar elemental content, and demography of *Thalassia testudinum* were monitored in populations from five sites across Florida Bay beginning in January 2001. Sites were selected to take advantage of the spatial variability in phosphorus (P) availability and salinity climates across the bay. Aboveground biomass and NPP of *T. testudinum* were determined five to six times annually. Short-shoot demography, belowground biomass, and belowground NPP were assessed from a single destructive harvest at each site and short-shoot cohorts were estimated from leaf scar counts multiplied by site-specific leaf production rates. Biomass, relative growth rate (RGR), and overall NPP were positively correlated with P availability. Additionally, a positive correlation between P availability and the ratio of photosynthetic to non-photosynthetic biomass suggests that *T. testudinum* increases allocation to aboveground biomass as P availability increases. Population turnover increased with P availability, evident in positive correlations of recruitment and mortality rates with P availability. Departures from seasonally modeled estimates of RGR were found to be influenced by salinity, which depressed RGR when below 20 psu or above 40 psu. Freshwater management in the headwaters of Florida Bay will alter salinity and nutrient climates. It is becoming clear that such changes

will affect *T. testudinum*, with likely feedbacks on ecosystem structure, function, and habitat quality.

Keywords Seagrass · Productivity · Demography · Phosphorus · Salinity · Long-term monitoring

Introduction

South Florida has a history of engineered land-use and water-use changes that have directly affected abiotic conditions in Florida Bay, which in turn have driven changes in the benthic ecosystems of the bay (Schmidt 1979; Zieman 1982; Brewster-Wingard and Ishman 1999; Fourqurean and Robblee 1999). Two such engineering projects include the Florida Overseas Railway (1907 to 1911) and a system of canals, levees, and water control structures (beginning in 1952) designed to prevent flooding and increase the amount of arable and habitable land in the Everglades (Light and Dineen 1994). Dredge spoil islands supporting the railway over the length of the Florida Keys have restricted circulation and water exchange between the Atlantic Ocean and Florida Bay (Swart et al. 1996) and diversion of freshwater from the Everglades to the Gulf of Mexico and Atlantic Ocean has reduced freshwater and organic matter delivery to the bay by approximately 60% (Smith et al. 1989). Changes in salinity and nutrient climates brought on by changes in circulation and freshwater delivery in the bay have caused reorganizations of benthic macrophyte communities, altering their structure, function, and quality as habitat for dependant species (Thayer et al. 1999; Butler et al. 2005; Armitage et al. 2005; Gil et al. 2006).

The seagrass *Thalassia testudinum* is the most abundant benthic macrophyte in Florida Bay and is known to respond

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sensitively to salinity (Quammen and Onuf 1993; Zieman et al. 1999; Lirman and Cropper 2003; Kahn and Durako 2006; Koch et al. 2007a), which is considered a likely cause of seagrass species distributions and distributional changes in the bay (Fourqurean et al. 2003b). In the 1960s and 1970s, seagrass communities in the northern and eastern parts of the bay were dominantly *Halodule wrightii* but are now sparse *T. testudinum* (Schmidt 1979; Zieman 1982). The shift in species dominance was attributed to increased and less variable salinity since the 1960s resulting from the diversion of freshwater flow (Fourqurean et al. 2003b). Evidence for the temporal change in salinity climate has been drawn from paleo-ecological reconstructions using stable isotope patterns in coral skeletons (Swart et al. 1996) and changes in benthic infauna from sediment cores (Brewster-Wingard and Ishman 1999).

Seagrass species distributions in Florida Bay are strongly influenced by nutrients. *T. testudinum* responds to increased nutrient availability with increases in aboveground biomass and productivity, but belowground allocations are poorly understood, an important knowledge gap considering that stored reserves in rhizomes may facilitate survival in periods of unfavorable conditions (Hemminga and Duarte 2000). Increased nutrient availability also facilitates the establishment of faster-growing species such as *H. wrightii* and *Ruppia maritima*, which can displace *T. testudinum* (Powell et al. 1989, 1991; Fourqurean et al. 1995; Armitage et al. 2005; Herbert and Fourqurean 2008). Because of this tendency for species shifts with nutrient supply, community composition throughout the bay is driven in part by a spatial pattern of P availability that clearly places limits on seagrass biomass and growth (Fourqurean and Zieman 2002; Armitage et al. 2005).

Because of the sensitivity of *T. testudinum* to salinity and nutrient supply, it is widely believed that changes in water delivery to Florida Bay via upstream management or climate change will alter its benthic ecosystems. Benthic macrophytes and associated epiphytic and epifaunal communities affect both ecosystem function and quality of habitat for dependant species (Butler et al. 2005; Armitage et al. 2005; Gil et al. 2006) and are likely to have a large impact on associated fish and invertebrate communities (Thayer and Chester 1989; Thayer et al. 1999). Consequently, water-quality-driven changes in benthic macrophyte communities could affect populations of game fish including sea trout, redfish, and snook; the commercial pink shrimp fishery in the Dry Tortugas that use Florida Bay as a nursery (Nance 1994); and several endangered species including the American crocodile and Florida manatee for which Florida Bay is primary habitat (McIvor et al. 1994).

With impending changes in salinity and nutrient climates, it is important to understand how biomass and growth of *T. testudinum*, both aboveground and below-

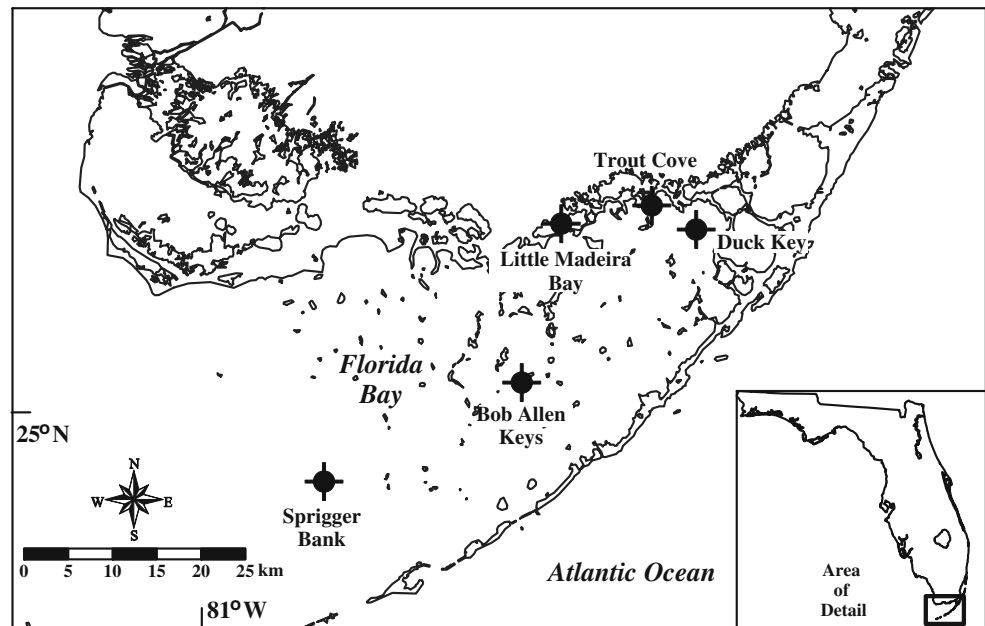
ground, change as a function of nutrients and salinity. To this end, we have analyzed long-term data spanning 7 years of biomass, density, and productivity measurements with respect to salinity and tissue nutrient content. The field sites, located in regions of Florida Bay that are spatially distinct in phosphorus (P) availability (Fourqurean and Zieman 2002) and salinity climates, have been carefully maintained as part of the Florida Coastal Everglades Long-Term Ecological Research Program. We examine relationships between aboveground and belowground standing crop, total biomass, productivity, and short-shoot demography and how these are modified by variability in P and salinity climates throughout Florida Bay.

Methods

T. testudinum growth rate, biomass, foliar elemental content, and short-shoot age structure were measured at five sites in Florida Bay (Fig. 1). The sites were selected to take advantage of the spatial variability in P availability and salinity climates across Florida Bay. Phosphorus availability decreases from southwest to northeast in the bay (Fourqurean et al. 1992), and in the northernmost reaches of the bay P availability is influenced by groundwater discharges having elevated total P concentrations (Price et al. 2006). Sprigger Bank (25° 54' N, 80° 56' W) is on the western open boundary between Florida Bay and the Gulf of Mexico and is the site with the most stable salinity and highest P availability (Frankovich and Fourqurean 1997). From January 2001 to September 2007, salinity ranged from 29.5 to 40.2 psu, averaging 35.7 psu. Bob Allen Keys (25° 01' N, 80° 40' W) and Duck Key (25° 10' N, 80° 29' W) are 29 and 55 km, respectively, NE of Sprigger Bank and have low P availability. Salinity is more variable at these sites, averaging 35.6 psu (22.0–46.9 psu) at Bob Allen Keys and 31.8 psu (13.5–45.0 psu) at Duck Key between January 2001 and September 2007. Little Madeira Bay (25° 11' N, 80° 38' W) and Trout Cove (25° 12' N, 80° 32' W) are respectively 14 km W and 5 km NW of Duck Key and are near the mangrove shoreline in the northernmost reaches of Florida Bay. These near-shore sites are strongly influenced by surface water and groundwater discharges from the Everglades. Consequently, the sites are intermediate in P availability and salinity varies widely, averaging 27.3 psu (3.1–47.6 psu) at Little Madeira Bay and 23.7 (0.01–45.7 psu) at Trout Cove between January 2001 and September 2007. Water depth at all sites is less than 2 m.

Field measurements were conducted from December 2000 to August 2007 at Sprigger Bank, Bob Allen Keys, and Duck Key and from June 2003 to August 2007 at Little Madeira Bay and Trout Cove. Surface salinity was

Fig. 1 Locations of the long-term seagrass monitoring sites in Florida Bay



measured during each site visit and the overall salinity climate was established with the use of long-term data archives that included locations within 200 m of each of our sampling points, maintained by the Water Quality Monitoring Network, Southeast Environmental Research Center, Florida International University and by Everglades National Park.

Aboveground Productivity, Leaf Emergence Rates, and Nutrient Analyses

In *T. testudinum*, only green leaves and inflorescences emerge from the sediment. Non-photosynthetic structures including roots, rhizomes, and short shoots (vertical leaf-bearing rhizomes) remain entirely buried. Therefore, aboveground biomass, net primary productivity (ANPP), and chemistry refer specifically to leaves. Leaf productivity measurements were conducted five to six times annually at each site. A modified leaf-marking technique was used to determine ANPP and new leaf emergence rates (Zieman 1974; Zieman et al. 1999). Six 10×20 cm quadrats were haphazardly distributed within 10 m of a permanent steel rod that marked the site. Within each quadrat, the leaves of all short shoots of *T. testudinum* were pierced with an 18-gauge hypodermic needle to mark where they emerge from the sediment. The marked short shoots were allowed to grow for 10–14 days, after which all aboveground seagrass material in the quadrats was harvested. Plant material was separated by seagrass species and *T. testudinum* leaves were separated further into newly produced (unmarked leaves and the portion of older leaves below the marks) and older leaf material. Short-shoots in each quadrat were counted, as were the number of leaves per short shoot, which were

measured (length and width to the nearest millimeter), cleaned of epiphytes by gentle scraping, and dried to constant mass at 70°C. We quantified standing crop as the dry weight of green leaves per square meter, areal leaf production as the dry weight of green leaves produced per square meter per day; and aboveground relative growth rate (aRGR) as dry weight of green leaves produced per gram of dry weight of green leaves per day.

The same leaf mark used to separate new growth from old growth for ANPP was used to determine the rate of new leaf production per short shoot. Leaf emergence rate (LER = new leaves per short shoot per day) was calculated by dividing the number of new leaves produced in the 10–14-day growth period by the total number of marked short-shoots, then dividing by the time interval between marking and harvest. Note that LER is the reciprocal of plastochron interval (PI) or the number of days between emergences of successive leaves on a short shoot (Patriquin 1973; Brouns 1985).

Cleaned and dried leaves were ground to a fine powder using a ceramic mortar and pestle and analyzed in duplicate for carbon and nitrogen content using a CHN analyzer (Fisons NA1500). Phosphorus content was determined by a dry oxidation, acid hydrolysis extraction followed by a colorimetric analysis of phosphate concentration of the extract (Fourqurean et al. 1992). Elemental content was calculated on a dry weight basis (i.e., mass of element/dry weight of sample×100%); elemental ratios were calculated on a mole–mole basis.

At each site, replicate measurements of aboveground seagrass parameters (density, biomass, growth, and nutrients) were reduced to a single mean per site visit. In Florida Bay, there is a seasonal pattern in seagrass

biomass and growth. Therefore, to avoid any bias due to date of sample, data were assessed by least-squares fitting of a sine function (Eq. 1):

$$Y = \bar{Y} + \alpha[\sin(\text{DOY} + \phi)], \quad (1)$$

where \bar{Y} is the estimated mean value of the time series; α is the amplitude of the sine wave fit through the time series, and ϕ is the phase angle that determines the timing of the peak in amplitude. Time was expressed as the day of year (DOY), converted to radians (2π radians=365 days; Fourqurean et al. 2001). $\bar{Y} \pm$ the 95% confidence interval (CI) describes the seasonally unbiased site mean and α describes the seasonal amplitude around Y . Regression analysis was used to compare site means for biomass and components of productivity with foliar nutrient concentration, the index of nutrient availability. Residual variation ($Y - \bar{Y}$) not explained by seasonality can be used to examine growth-limiting factors that might cause deviations from seasonally predicted growth. Here, we examine the effects of high- and low-salinity events on aRGR. We identified high- and low-salinity events as those growth measurement intervals during which salinity exceeded 40 psu or was less than 20 psu for 50% or more of the measurement interval. These are extremes supported by earlier research (Zieman et al. 1999; Lirman and Cropper 2003; Koch et al. 2007a). One-way analysis of variance with multiple pairwise comparisons of means were applied to test for differences in the residuals for high-, low-, and intermediate-salinity (30–40 psu) events. Residuals were standardized to observations (residual/observed aRGR) so as not to bias the analysis with differences in site-specific aRGR. Sprigger Bank was excluded from this analysis because a continuous salinity record is not available for the site. Furthermore, the salinity range recorded during sampling periods (29.5 to 40.2 psu) is not wide enough to test the hypothesis of diminished aRGR in response to high- and low-salinity events. Large residuals at Sprigger Bank would be due to other growth-limiting factors such as high- and low-temperature events.

Demographics: Determining Age Structure

On May 14, 2007, samples were collected for *T. testudinum* demographic analyses. Populations of short shoots from each site were collected by excavating a sod that contained >100 short shoots, approximately 0.5 m² to a depth of 15 cm, except where limited by bedrock. Small losses of roots growing into limestone may have resulted in an underestimate of root mass at Duck Key and Bob Allen Banks. The root–rhizome complex was gently washed to remove sediment then placed in sealed plastic bags and returned to the laboratory for processing. All

short-shoots collected, whether attached or unattached to a rhizome, were included in the analysis. The number of leaves produced over the lifespan of each short shoot in a sample was determined by counting leaf scars and extant green leaves. Short-shoot age was estimated by the number of leaves produced by a short-shoot, scaled by the site-specific annual leaf production rates as determined from the analysis of short-shoot marking at the sites (Patriquin 1973; Duarte et al. 1994). Short-shoot age frequency distributions were derived from the number of short-shoots in 6-month age classes. From these age frequency distributions, we estimated the long-term per capita mortality rate, M , by using regression to fit (Eq. 2) to the age frequency distributions:

$$N_x = N_0 e^{-Mx}, \quad (2)$$

where N_0 is the estimated number of short shoots in the youngest age class and N_x is the number of short shoots in the x th age class (Fourqurean et al. 2003a). This regression approach assumes that M and the per capita recruitment rate, R , have had no trend over the life span of the oldest short shoots in the population and that $R=M$, i.e., the population is at equilibrium. The 95% confidence limits of the value of M (and therefore R) at each site were calculated from the regression and were used to determine if current-year recruitment, R_0 , was different from the long-term average, sampled as (Eq. 3):

$$R_0 = \ln N_t - \ln N_{x>1}, \quad (3)$$

where N_t is the total number of short shoots in the population and $N_{x>1}$ is the number of short shoots older than 1 year. The use of age frequencies to estimate rates of mortality and recruitment has been questioned because underlying assumptions are biased against rapidly growing or declining populations (Jensen et al. 1997; Kaldy et al. 1999; Ebert et al. 2002; Fourqurean et al. 2003a). However, long-term monitoring indicates no long-term trend in short-shoot density at all sites. Therefore, the assumption of $R=M$ is reasonable in this case. Regression analysis was used to compare site estimates of M and R_0 with foliar nutrient concentration, standing crop, and productivity.

Belowground Biomass and Productivity

Non-photosynthetic biomass (belowground) including roots, rhizomes, and defoliated short shoots was measured from the same excavated sod used to determine age structure. The sod was washed and dried to constant mass at 70°C. Belowground net primary productivity (BNPP) was estimated from site-specific per capita gross short-

shoot recruitment rates, R_G , which adjusts R to account for mortality of short shoots aged <1 year (Eq. 3):

$$R_G = \frac{\sum_{j=1}^k e^{(\ln n_j + M_j t)} N}{N}, \quad (4)$$

where n is the number of short shoots in the j th age class; t is the age of the j th age class; k is the oldest age class <1 year; M is per capita mortality rate from Eq. 2, and N is the total number of short shoots in all age classes (Peterson and Fourqurean 2001). Belowground mass per short-shoot was multiplied by R_G for the BNPP estimate. This and comparable methods for estimating belowground production have been applied to a variety of seagrass species (Pergent-Martini and Pergent 2004; Duarte et al. 1998; Guidetti et al. 2000; Calvo et al. 2006). Regression analysis was used to compare belowground components of biomass and productivity with foliar nutrient concentration.

Results

Foliar P concentrations varied widely (~270%) among sites but foliar N varied little (~22%, Table 1). In common with earlier investigations of nutrient limitation in Florida Bay (Fourqurean et al. 1992; Frankovich and Fourqurean 1997), we found that aboveground biomass of *T. testudinum* increased with foliar P concentration ($r^2=0.93$, $p=0.008$) as did average leaf mass per short shoot ($r^2=0.92$, $p=0.010$). Relationships with foliar N concentration were negative but significant, indicating a dilution effect with increasing leaf mass. The range of foliar N concentration suggests no limitation by N (Fourqurean et al. 1992). For these reasons, we have focused on P as the nutrient-limiting biomass and growth at the study sites.

Seasonality, Salinity, and P Availability Influence Aboveground Productivity

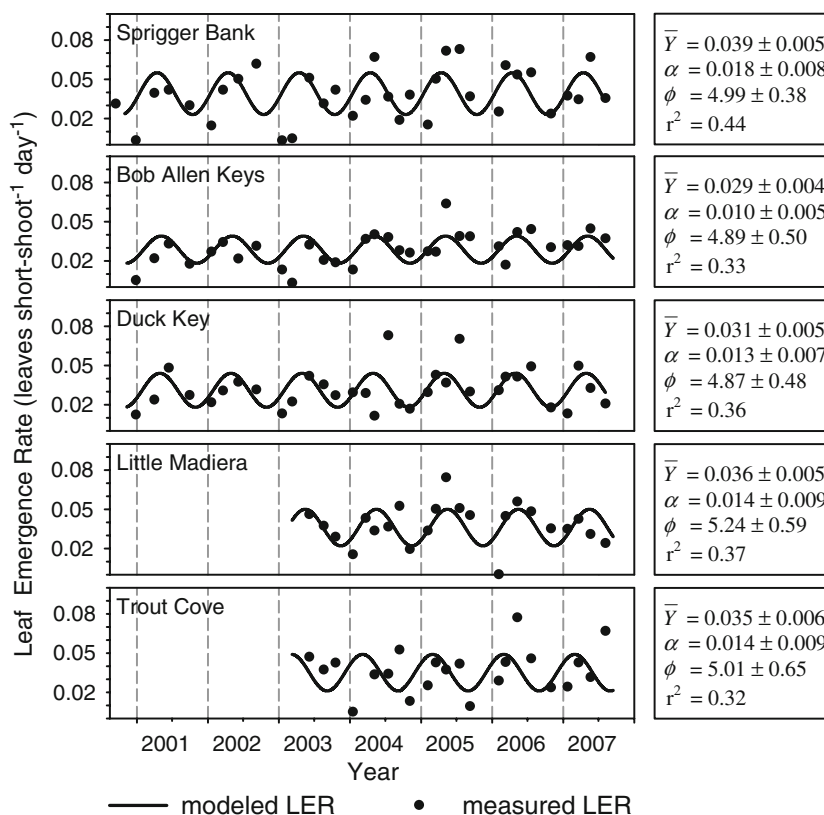
An absence of long-term trends in short-shoot density in all sites indicates that sampling methods did not affect long-term patterns in biomass and productivity. The sine model (Eq. 1) described seasonal patterns in several components of productivity including LER (leaves per short shoot per day), aRGR ($\text{mg g}^{-1} \text{day}^{-1}$), and ANPP ($\text{g m}^{-1} \text{day}^{-1}$), with maxima in summer and minima in winter at all sites. Site-specific modeled LER explained 32% to 44% of the annual variance in measured LER, which ranged from a yearly $\overline{\text{LER}}$ of 0.029 leaves per short shoot per day ± 0.004 (which is equivalent to a PI=34.5 day) at Bob Allen Keys to 0.039 leaves short per shoot per day ± 0.005 (PI=26.3 days) at Sprigger Bank (Fig. 2). There were marked differences between winter minima and summer maxima in LER; for example, at Sprigger Bank, LER was slower than the mean annual LER by 0.018 leaves per short shoot per day in winter and that much faster in summer. The seasonal amplitude, α_{LER} (from Eq. 1), at a site was positively correlated with $\overline{\text{LER}}$ ($r^2=0.89$, $p=0.015$) and averaged 40.3% (SE=1.9) of $\overline{\text{LER}}$, ranging from 36.4% of $\overline{\text{LER}}$ at Bob Allen Keys to 42.6% of $\overline{\text{LER}}$ at Sprigger Bank (46.2%). The large seasonal ranges of LER within sites translated to a PI of 17.5 days in the summer and 47.6 days in the winter at Sprigger Bank, while at Bob Allen Keys the summer PI was 25.4 days and winter was 53.8 days. Integrated over the year, Sprigger Bank produced an average 14.2 leaves per short shoot and Bob Allen Keys produced an average 10.4 leaves per short shoot, a 27% difference in the rate of leaf initiation. Across sites both, $\overline{\text{LER}}$ and α_{LER} were positively correlated with mean annual foliar P concentrations ($\overline{\text{LER}}$: $r^2=0.77$, $p=0.050$; α_{LER} : $r^2=0.77$, $p=0.051$). Analyses of the residual difference be-

Table 1 Shoot density and dry mass

Site	Foliar P (%)	Foliar N (%)	Density (shoots m ²)	Dry mass (milligram per ramet)				Total dry mass (g m ⁻²)	P _s biomass ratio
				Leaves	Short-shoots	Rhizome	Roots		
Sprigger Bank	0.134 (0.131–0.138)	2.05 (1.98–2.11)	221 (189–253)	213 (187–240)	71.6	355	36.7	148	0.447
Bob Allen Keys	0.061 (0.058–0.063)	2.53 (2.46–2.59)	295 (264–317)	54.1 (46–62)	62.1	227	18.4	104	0.167
Duck Key	0.050 (0.048–0.052)	2.31 (2.25–2.37)	612 (554–671)	30.8 (25–36)	38.1	167	35.4	165	0.126
Little Madeira	0.078 (0.073–0.083)	2.29 (2.21–2.37)	525 (437–612)	55.6 (48–64)	28.7	153	18.2	134	0.282
Trout Cove	0.085 (0.078–0.091)	2.46 (2.34–2.57)	470 (361–580)	59.9 (47–73)	79.3	153	41.8	158	0.227

P_s biomass ratio is the ratio of aboveground leaf mass to belowground root, rhizome, and short-shoot mass. Values in parentheses are 95% confidence intervals and are available only for variables obtained by long-term census. Leaves represent all aboveground biomass. Roots, rhizomes, and short shoots are considered belowground biomass. Values without confidence intervals include belowground biomass measurements, which were collected during a single destructive sample at each site

Fig. 2 Leaf emergence rates (LER) for *T. testudinum* at each of the sites. LER was determined by fitting least-squares sine functions to long term census data so as not to bias by the sample collection date (Eq. 1). $\bar{Y} = \overline{LER}$ of the time series, α = amplitude, and ϕ = phase angle. The \pm is the 95% confidence interval



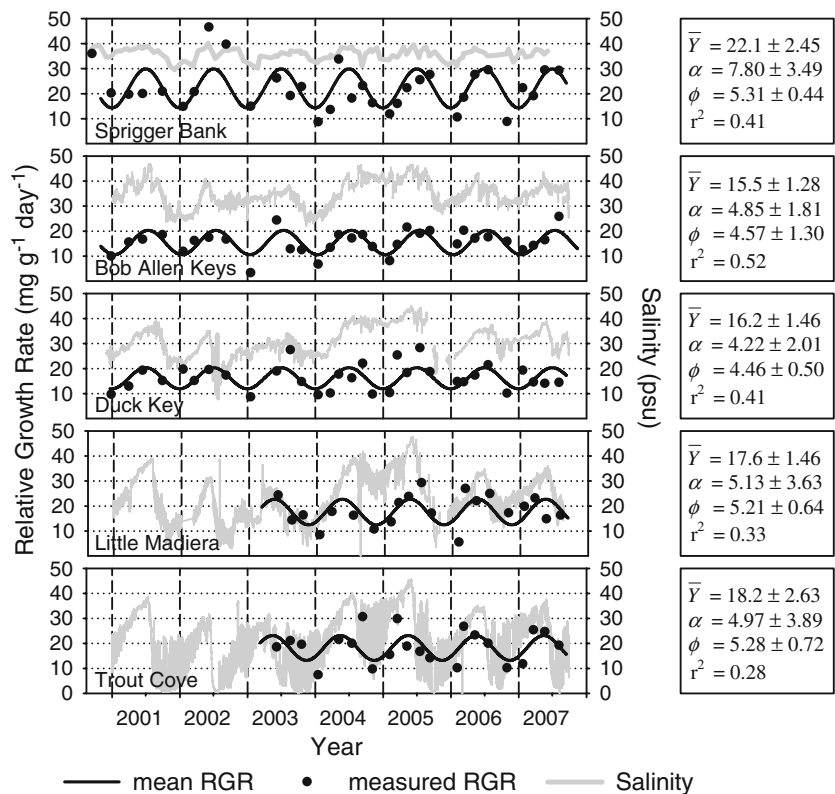
tween modeled LER and measured LER indicated no influence of random variations in salinity on model precision.

Modeled aRGR explained 28% to 46% of annual within-site variance. Across sites, aRGR ranged from $15.5 \text{ mg g}^{-1} \text{ day}^{-1} \pm 1.36$ at Bob Allen Keys to $22.0 \text{ mg g}^{-1} \text{ day}^{-1} \pm 2.60$ at Sprigger Bank (Fig. 3). Within-site aRGR was also highly seasonal. The amplitude of seasonal variation at a site, α_{aRGR} , was positively correlated with $\overline{\text{aRGR}}$ ($r^2=0.91$, $p=0.012$), and on average α_{aRGR} was 29.7% (SE=1.7) of $\overline{\text{aRGR}}$. Seasonal aRGR ranged from $30.1 \text{ mg g}^{-1} \text{ day}^{-1}$ in the summer to $14.2 \text{ mg g}^{-1} \text{ day}^{-1}$ in the winter at Sprigger Bank, and at Bob Allen Keys the summer maximum was $20.1 \text{ mg g}^{-1} \text{ day}^{-1}$ and winter minimum was $10.8 \text{ mg g}^{-1} \text{ day}^{-1}$. The predictive precision of modeled aRGR declined when measurements corresponded with extreme-salinity events. Analyses of the residual difference from measured aRGR indicate that when salinity was less than 20 psu aRGR was depressed (Fig. 4). There is evidence for similarly depressed aRGR when salinity exceeds 40 psu but the relationship is statistically weak. However, as with LER, foliar P concentration was the best predictor for aRGR (Fig. 5) and α_{aRGR} ($r^2=0.95$, $p=0.005$).

Short-shoot density (short shoots per square meter) and mass of short shoots were not seasonally dependent. Consequently, aRGR and ANPP were highly correlated

($r^2=0.99$, $p<0.001$). Modeled ANPP explained 31% to 51% of variance in measured ANPP at four of the sites but only 10% of variance at Little Madeira, where the model failed to describe a significant seasonal pattern. The reason for the disparity at Little Madeira is not clear but may be associated with leaf losses during extreme-salinity, temperature, wind, or perhaps grazing events. A positive correlation between residual ANPP and aboveground biomass at Little Madeira ($r^2=0.67$, $p<0.001$) provides evidence for the leaf loss explanation. ANPP ranged from $88.3 \pm 13.1 \text{ g m}^{-2} \text{ year}^{-1}$ at Bob Allen Keys to $349.7 \pm 62.1 \text{ g m}^{-2} \text{ year}^{-1}$ at Sprigger Bank and was positively correlated with P availability across sites (Fig. 5). The seasonal amplitude, α_{ANPP} , was not correlated with ANPP because of a very low α_{ANPP} at Little Madeira, where we have speculated on disturbance-caused leaf losses. The seasonal amplitude, α_{ANPP} , normalized by the mean, ANPP, varied widely, and with the exception of Little Madeira, increased as the seasonal variability in salinity climate increased (Fig. 6). This suggests that variability in salinity has lowered ANPP because of the frequency of growth-limiting salinity events resulting in larger than otherwise expected seasonal amplitudes. Sprigger Bank does not experience extreme-salinity events and, therefore, has the lowest α_{ANPP} relative to ANPP. Residual analyses of ANPP indicate that site-

Fig. 3 Salinity and aboveground relative (aRGR) growth rate of *T. testudinum* at each of the sites. aRGR was determined with Eq. 1 as in Fig. 2. $\bar{Y} = \overline{aRGR}$ of the time series, α = amplitude, and ϕ = phase angle. The \pm is the 95% confidence interval



specific deviations from predicted seasonal patterns could not be explained by salinity.

Standing crop (g m^{-2}) varied between sites and, like LER, aRGR, and ANPP, was positively correlated with

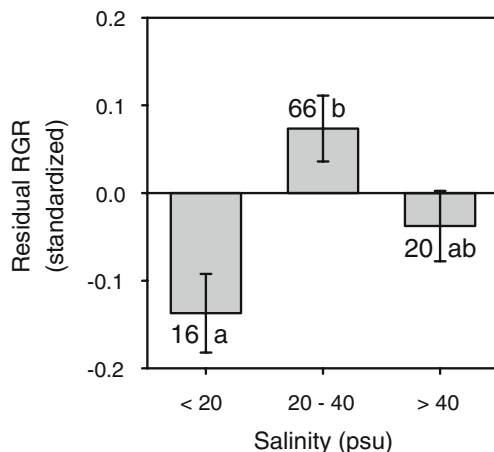


Fig. 4 The residual difference between measured aboveground relative and predicted aRGR at the Bob Allen Keys, Duck Key, Trout Cove, and Little Madeira sites where salinity fluctuated widely. Classes are defined as <20 or >40 psu during at least 50% of the growth period, and 20–40 psu during more than 50% of the growth period. Residuals have been standardized (residual–observed) to avoid biasing by differences in site-specific aRGR. Bars below the zero reference line indicate a depressed aRGR. Whiskers represent standard error. Letters indicate distinct groups based on Duncan-Waller comparison of means. Values next to bars represent the sample size

foliar P concentration (Fig. 5). Aboveground measures of growth and productivity were also correlated with standing crop (LER $r^2=0.939$, $p=0.007$; ANPP $r^2=0.995$, $p<0.001$; aRGR $r^2=0.975$, $p=0.002$), clearly pointing to the importance of P availability in the control of *T. testudinum* standing crop and function at the sites.

Short-Shoot Demography

The age characterization of short-shoots and site-specific population age structures were determined from site-specific PI ($1/\text{LER}$) and the number of leaf scars plus green leaves per short shoot. The longest-lived individual short shoots were determined to be as old as 10 years but population age structure varied widely among sites (Fig. 7). Per capita mortality (M , Eq. 2) ranged from a low of $0.27 \text{ year}^{-1} \pm 0.09$ (95% CI) at Bob Allen Keys to a high of $0.81 \text{ year}^{-1} \pm 0.25$ at Sprigger Bank. Recruitment of new short shoots within the last year (R_0 , Eq. 3) at three of the sites was within the 95% CI estimated for long-term M and therefore long-term recruitment (Eq. 2, assuming $M=R$). At Duck Key and Trout Cove, there is an indication of elevated R_0 (Fig. 3). However, no long-term trend in short-shoot density was detected in direct censuses at the sites, which provides a basis for the assumption of $M=R$ in the derivation of belowground production estimates.

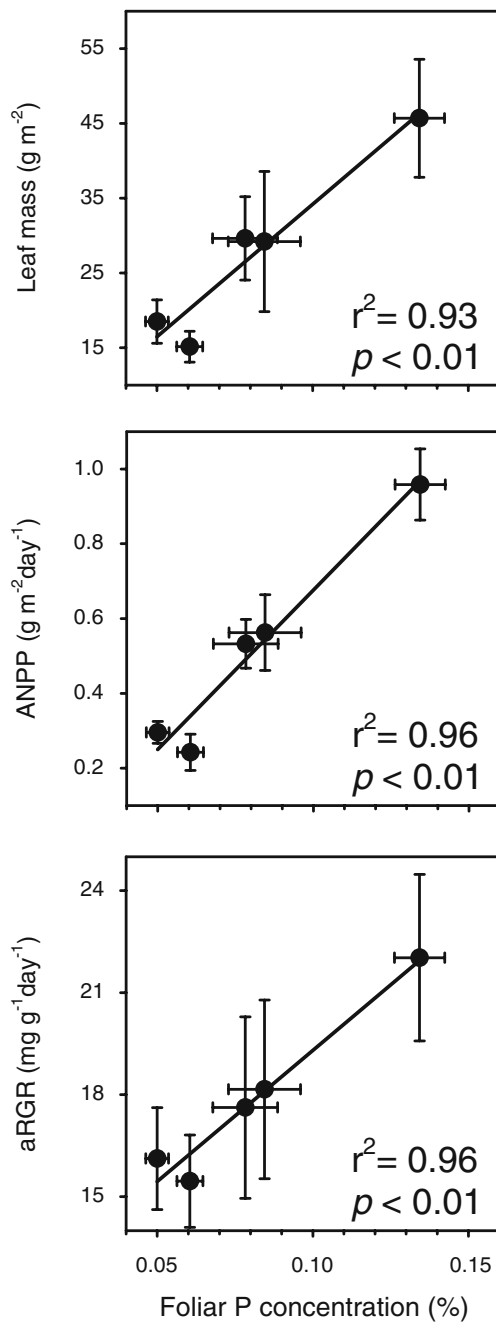


Fig. 5 Foliar P concentration influences aboveground biomass (leaf mass), aboveground net primary productivity (ANPP), and aboveground relative growth rate (aRGR). Vertical and horizontal whiskers represent 95% confidence intervals derived from least-squares sine functions fitted to long-term census data having strong seasonal patterns

Belowground Biomass, Belowground Productivity, and Contributions to NPP

Belowground non-photosynthetic structures made up as little as 69% of *T. testudinum* biomass at Sprigger Bank

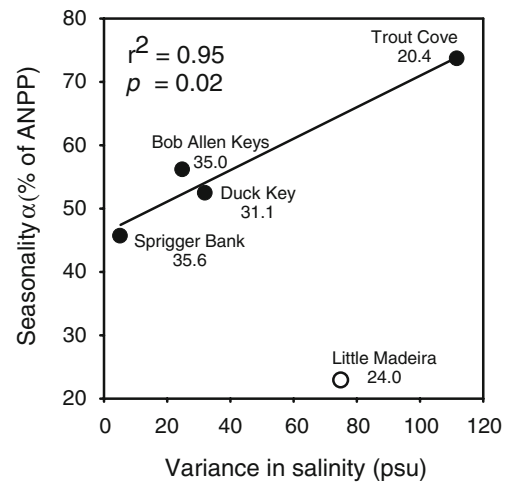


Fig. 6 ANPP seasonality expressed as the amplitude (α) percentage of \overline{ANPP} (Eq. 1) increases with the site-specific variance in salinity increases. Values associated with site names represent mean annual salinity (psu). The open symbol represents an outlier with no seasonality in ANPP, as described in results

and as much as 89% at Duck Key (Table 1), but salinity and P availability gradients across sites did not affect the quantity of belowground biomass in a predictable manner. There was, however, a clear pattern in biomass allocation relative to foliar P (Fig. 8) evident as the ratio of leaf mass to belowground non-photosynthetic mass (photosynthetic biomass ratio, PBR). The positive relationships of PBR with P availability suggests that *T. testudinum* invests in the production of photosynthetic tissues proportionately with P availability and when P is limiting it invested in belowground structures to maximize nutrient capture.

BNPP was not correlated with foliar P concentration ($r^2=0.60, p=0.123$) but was positively correlated with standing crop ($r^2=0.83, p=0.030$) and ANPP ($r^2=0.79, p=0.044$), suggesting that the coincidence of elevated BNPP with increased P availability is a real effect. Belowground RGR was positively correlated with P ($r^2=0.78, p=0.047$), standing crop ($r^2=0.93, p=0.008$), and ANPP ($r^2=0.89, p=0.016$), providing additional evidence for the coupling of aboveground and belowground processes.

Overall, total (above + belowground) NPP ($\text{g m}^{-2} \text{ day}^{-1}$) and RGR ($\text{mg g}^{-1} \text{ day}^{-1}$) were positively correlated with foliar P (Fig. 8) and with standing crop (NPP: $r^2=0.998, p<0.001$; RGR: $r^2=0.941, p=0.006$). Despite the contribution of the non-photosynthetic structures to total biomass, NPP was dominated by leaf production. BNPP contributions to NPP averaged $0.20 \text{ g m}^{-2} \text{ day}^{-1}$, ranging from $0.02 \text{ g m}^{-2} \text{ day}^{-1}$ at Bob Allen Keys to $0.29 \text{ g m}^{-2} \text{ day}^{-1}$ at Sprigger Bank (Fig. 9). As a percentage of NPP, BNPP represented 23% to 37% of NPP, averaging 28.4% (SE=0.026) across sites.

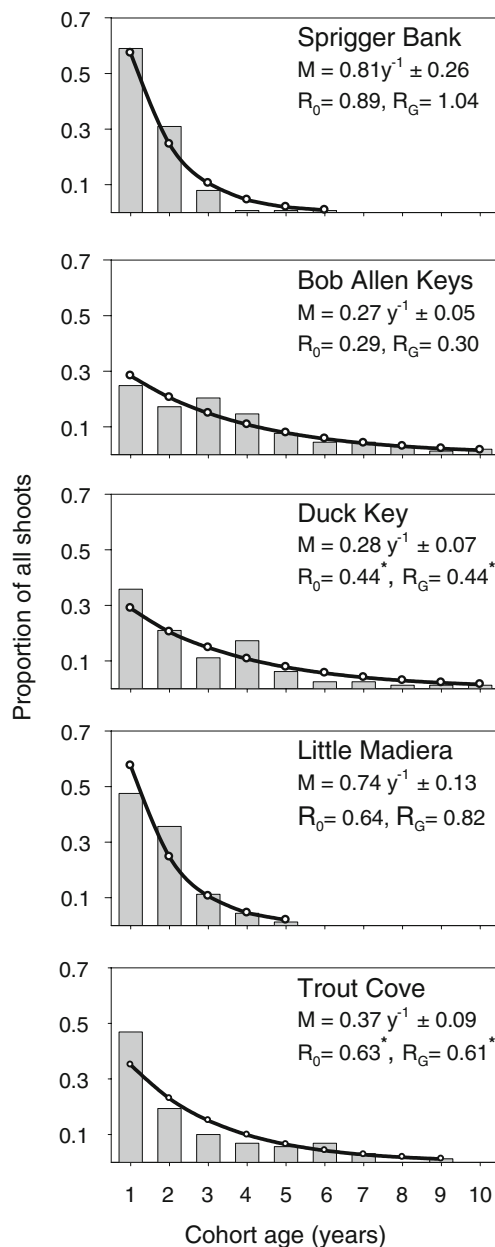


Fig. 7 Age structure of *T. testudinum* populations reconstructed from leaf emergence rates and leaf scar counts in populations of short shoots. Age classes represent 1-year cohorts; M is the mortality rate estimated from 0.5-year age classes and R_0 is the recruitment rate of cohorts <1 year old. R_G is the recruitment rate adjusted for mortality in age classes <1 year old. Confidence intervals are derived from regression analysis on 0.5-year age classes. Asterisks indicate that R_0 is significantly different from M

P Availability Controls Demography

Long-term M (and therefore R) and the shorter-term R_0 were positively correlated with total NPP and standing crop (Fig. 10). Direct correlations with foliar P concentrations were also significant (R_0 : $r^2=0.82$, $p=0.04$; M : $r^2=0.65$, $p=0.10$). The results suggest an inverse short-shoot life span relationship with biomass and/or productivity, which points

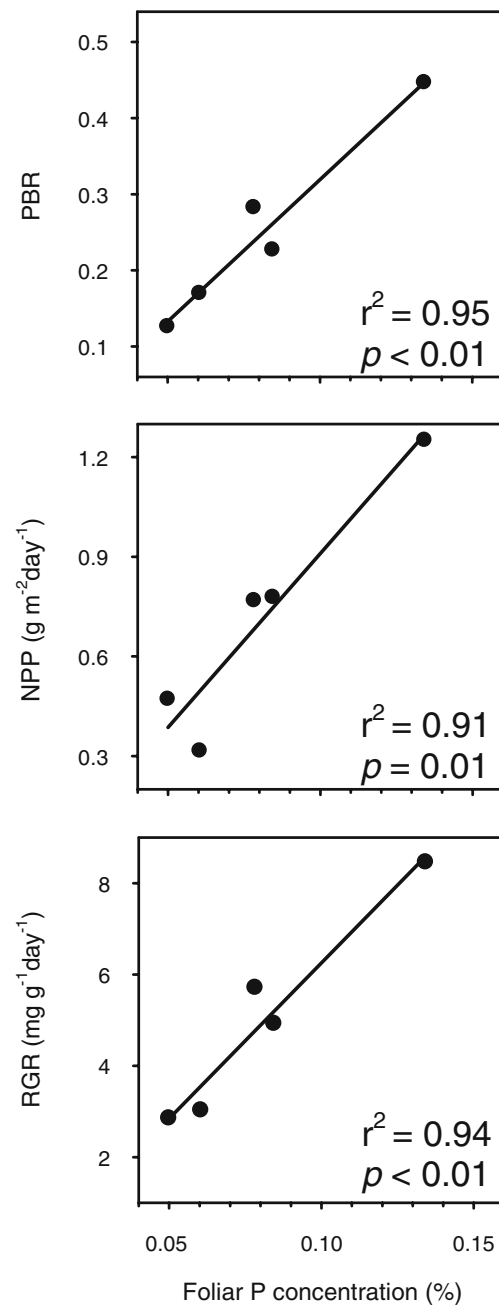


Fig. 8 Foliar P concentration influences on biomass allocation and production inclusive of belowground components. Panels include photosynthetic biomass ratio (PBR, the ratio of aboveground to belowground mass), primary productivity (NPP), and relative growth rate (RGR)

to P availability as being a key factor underlying the age structure and turnover rates of *T. testudinum* populations in Florida Bay. Average short-shoot life spans are generally shorter in relatively high-P environments and longer in low-P environments. A positive correlation between M and LER ($r^2=0.84$, $p=0.045$) suggests that higher leaf turnover rates associated with greater P availability may play a role in the observed turnover rates in short-shoot populations.

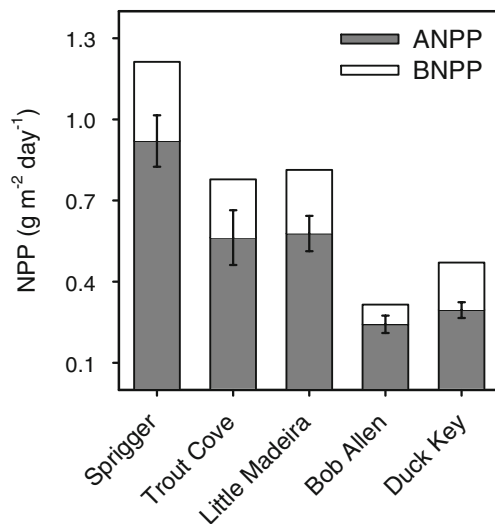


Fig. 9 Net primary productivity of *T. testudinum* distinguishing aboveground (ANPP) and belowground (BNPP) allocation. From left to right, sites are organized by decreasing foliar P concentration. BNPP is correlated with ANPP ($r^2=0.78$, $p=0.048$)

Discussion

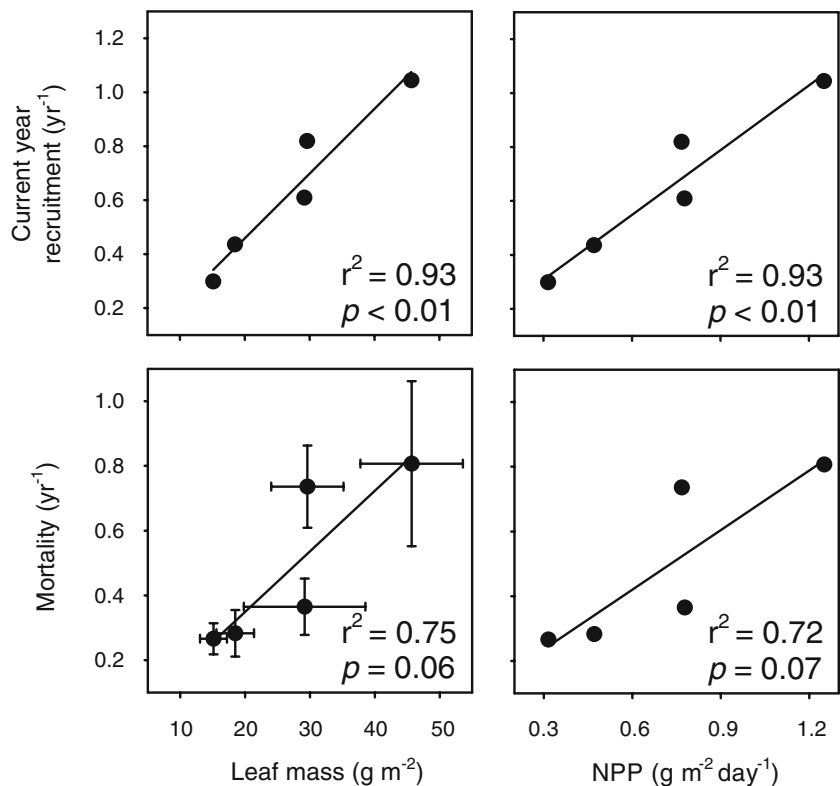
Long-term monitoring at five sites representing a broad and naturally occurring range in phosphorus availability and salinity climates has provided insight into the regulatory role of these two abiotic factors in *T. testudinum* populations across Florida Bay. Biomass, productivity, and

population turnover rates change predictably with P availability and deviations from these relationships can be explained, in part, by salinity.

Foliar P concentrations, used as a proxy for P availability, were consistent with earlier characterizations of P availability decreasing from West to East across Florida Bay (Fourqurean et al. 1992; Fourqurean and Zieman 2002) with the exception of sites very close to the mangrove shorelines in the northernmost reaches of the bay. At those sites, foliar P concentrations were elevated relative to the large-scale P availability gradient suggesting elevated P availability, despite the very low concentrations of P in the surface waters flowing into Florida Bay (Rudnick et al. 1999). It is likely that this increase in P availability is a result of the discharge of P-enriched groundwater along the mangrove-lined coast, which supplies as much P as Taylor Slough, the main contributor of surface water runoff to Florida Bay (Price et al. 2006).

The effect of increased P availability on the biomass of *T. testudinum* was to increase standing crop. The relationship between standing crop and P availability is consistent with earlier investigations in Florida Bay (Fourqurean et al. 1992). In contrast, there was no apparent effect of P availability on belowground biomass, which comprised 69% to 89% of the total. However, there was a strong and positive relationship in the ratios of aboveground versus belowground biomass with P availability. These lines of evidence suggest that *T. testudinum* invests in the produc-

Fig. 10 Mortality and recruitment of current-year cohorts (individuals <1 year old) are correlated with aboveground mass (leaf mass) and net primary productivity (NPP) including aboveground and belowground components. Vertical and horizontal whiskers represent 95% confidence intervals as derived in Figs. 3, 4, and 5. Points without confidence intervals combine directly sampled data with population reconstruction data. Recruitment lacks confidence intervals because it is based on cohorts younger than 1 year



tion of photosynthetic tissues proportionately with nutrient availability. This adds to existing theory and evidence that plants invest carbon and effort into aboveground and belowground structures proportionally to resource supply to improve acquisition of limiting resources, i.e., nutrient-sufficient plants invest in leaf area and/or photosynthetic capacity while nutrient-limited plants invest in nutrient acquisition and storage (Chapin 1980; Gower 1987; Tilman 1988; Herbert et al. 2004).

Increases in LER, aRGR, and ANPP were also positively correlated with P availability. Values reported here for Florida Bay were comparable to those recorded in earlier investigations in south Florida. The cross-site average LER (0.034 ± 0.005 leaves per short shoot per day) was comparable to the cross-site average reported by Peterson and Fourqurean (2001) for 28 sites in the Florida Keys National Marine Sanctuary (FKNMS) on the Atlantic side of the Florida Keys and in the Gulf of Mexico ($\overline{\text{LER}} = 0.030 \pm 0.005$ leaves per short shoot per day). However, the average seasonality in Florida Bay (41% of $\overline{\text{LER}}$) was larger than reported for FKNMS (33% of $\overline{\text{LER}}$) and may be attributed to the estuarine nature of Florida Bay and a larger annual temperature variation associated with shallow depths and long water residence time (Schomer and Drew 1982). The cross-site average aRGR ($17.9 \text{ mg g}^{-1} \text{ day}^{-1}$) and seasonality (30% of aRGR) in Florida Bay was nearly identical to those measured in the FKNMS where aRGR averaged $18.2 \text{ mg g}^{-1} \text{ day}^{-1}$ and seasonality averaged 31% of aRGR (Fourqurean et al. 2001). The range that we report for aRGR is encompassed by earlier reports from eastern Florida Bay ($14.8 \text{ mg g}^{-1} \text{ day}^{-1}$; Zieman et al. 1999) and Biscayne Bay to the northeast ($21.5 \text{ mg g}^{-1} \text{ day}^{-1}$; Zieman 1974). Our estimates of ANPP (88 to $350 \text{ g m}^{-2} \text{ year}^{-1}$) were also comparable to prior measurements, which have ranged from $59 \text{ g m}^{-2} \text{ year}^{-1}$ in the northeastern region of the Bay to $111 \text{ g m}^{-2} \text{ year}^{-1}$ in the east central region (Zieman et al. 1989, 1999) to an average $256 \text{ g m}^{-2} \text{ year}^{-1}$ in the FKNMS (Fourqurean et al. 2001).

The positive correlations of LER, aRGR, and ANPP with P have not been previously reported, but the regulatory role of P on aRGR and ANPP has been inferred by positive correlations with standing crop (Fourqurean et al. 1992, 2001). As in those investigations, we found that standing crop was a good predictor of aRGR and that it was also a good predictor of LER. The relationships of LER with P availability and standing crop are important as a mechanism to increase productivity, implicating increased leaf turnover rates and not simply increased leaf size and photosynthetic capacity. In fact, while seagrasses are known to be phenotypically plastic in their photosynthetic capacity (Collier et al. 2008), there is little evidence that mass-specific photosynthetic capacity of their leaves is affected by nutrient availability (but see Alcoverro et al. 2001) as is

the case for many terrestrial plants (Reich et al. 1991). The relationship between leaf turnover rate and nutrient supply is well established in terrestrial plant ecology (Chapin 1980; Chabot and Hicks 1982; Reich et al. 1991) and has been recorded across naturally occurring nutrient gradients, including P gradients (Herbert and Fownes 1999). Typically, plants replete with nutrients have leaves with short life spans and greater mass-specific photosynthetic capacity, while those stressed by nutrient limitation invest in longer-lived leaves that have a lower mass-specific photosynthetic capacity. In seagrasses, the photosynthetic capacity of longer-lived leaves is likely to be reduced by the accumulation of epiphytes.

Because seagrass roots, rhizomes, and the vertical leaf-bearing short shoots are typically buried, a complete assessment of the contribution of *T. testudinum* to ecosystem function requires measurements of belowground productivity. Our population reconstructions indicated that two of the sites had an increased rate of short-shoot recruitment in the youngest annual cohort suggesting population growth ($M \neq R$), which invalidates method assumptions. However, occasional recruitment highs and lows were also evident among older cohorts (Fig. 6) and long-term monitoring indicated unchanging short-shoot densities at all sites during 4 to 7 years of monitoring. This is important to the present study for two reasons. First, we can assume that current belowground biomass allocation is representative of longer-term conditions, which makes it possible to estimate belowground productivity to compliment direct measurements of aboveground productivity. Second, we can assume that the structural and functional entities measured are in an approximate equilibrium state with abiotic conditions and can be considered end point rather than transitional responses to present-time abiotic conditions, which may have been altered by past water management decisions affecting upstream sources in the Everglades.

In earlier BNPP measurements for *T. testudinum*, the belowground allocation has been about 33% of NPP (Patriquin 1973; Kaldy and Dunton 2000). In ^{14}C -labeled CO_2 incubations (4 h) with *T. testudinum*, Bittaker and Iverson (1976) found that C apportionment was 27.7% to roots and rhizomes. Our measurements of BNPP in Florida Bay (23% to 37% of NPP) were comparable to these earlier measurements and added 27 to $107 \text{ g m}^{-2} \text{ year}^{-1}$ to areal productivity. ANPP and BNPP were positively correlated, but BNPP and the ratio of ANPP to BNPP were unaffected by P availability indicating that allocation to BNPP may be limited by the imposed respiration burden of non-photosynthetic belowground structures (Fourqurean and Zieman 1991). Increased allocations to photosynthetic tissues with increased P availability translated to overall increases in RGR and NPP and point to P availability as the most

important factor controlling the magnitude of *T. testudinum* functions at the study sites.

The age structure of a population reflects past recruitment and mortality rates (Caswell 1989). Mortality and recruitment estimates of *T. testudinum* in Florida Bay indicate that elevated P availability produces a population structure characterized by populations of short shoots with younger average ages, high productivity, and high turnover rates. P-limited sites were characterized by populations with comparatively low productivity and turnover rates. This suggests that high resource availability may function to intensify intraspecific competition as new recruits increase short-shoot density and standing crop, thus increasing *M*. An earlier examination of *T. testudinum* population structure in the FKNMS revealed that there were no statistically significant relationships between demography and depth or light reaching the bottom (Peterson and Fourqurean 2001). This lack of correlation suggests that the amount of light reaching the bottom is not the only controller of recruitment and mortality. Our results point to nutrient availability, specifically P, as an important control on age structure and turnover of *T. testudinum* populations in Florida Bay.

While biomass, productivity, and demography changed predictably with P availability, deviations from predicted patterns were explained, in part, by salinity. Depressed productivity in *T. testudinum* has been measured following experimental low-salinity pulses (Lirman and Cropper 2003). Our results indicate similar depressions in aRGR following low-salinity events and the responses were consistent over 4 to 7 years of monitoring. Hypersaline conditions that periodically occur in Florida Bay (Fourqurean and Robblee 1999) also depressed aRGR but the relationship was statistically weak. The detrimental effect of high salinity on ANPP has strong support from earlier investigations elsewhere in Florida Bay and Biscayne Bay (Zieman et al. 1999; Lirman and Cropper 2003; Koch et al. 2007a).

Salinity also affected seasonality (site-specific amplitude–mean) of ANPP. While the mean site-specific LER, aRGR, and ANPP all increased with P, seasonality of LER and aRGR was a constant percentage of mean LER and aRGR, respectively. However, seasonality of ANPP varied widely and was positively correlated with the variance in salinity at a given site. Productivity is at its peak in the summer when irradiance and temperatures are optimum for growth, but this coincides with the rainy season when low-salinity events are likely to slow or stop growth. The result is depressed mean ANPP and wide amplitude relative to ANPP in regions of Florida Bay that regularly experience such low-salinity events. Interestingly, the effect did not show up in aRGR suggesting that the low-salinity events may have caused short-shoot deaths. The relationship between ANPP and the variability of salinity climate adds

support for the productivity-depressing effect of extreme-salinity events, but because the effect was not seen in aRGR it is evident that recovery from the depression of growth rate (Fig. 4) is rapid, allowing populations to persist in areas with highly variable salinity climates. Despite the demonstrated effects that salinity and its variability have on the growth of *T. testudinum*, short-shoot life span and mortality were not correlated with either mean salinity or salinity variability. Perhaps this is because of the overriding influence that P availability has on short-shoot life span in this oligotrophic environment.

Nutrient and salinity climates in Florida Bay are expected to change in response to upstream water management in the Everglades. Overland (sheet) water flow through the Everglades is essentially scrubbed of P, so increases in sheet flow will not add to P availability (Rudnick et al. 1999), but an increase in hydrologic head in the mangrove ecosystems can be expected to increase P delivery to near-shore regions of the bay via groundwater transport (Price et al. 2006). Increases in both sheet and groundwater flow will decrease salinity and its variability in the near-shore basins. Across the bay, there is a strong gradient in P availability, which decreases from southwest to northeast (Fourqurean et al. 1992), and it is known that the distribution of seagrass species is associated with both the supply of P and with salinity (Fourqurean et al. 2003b). *T. testudinum* is the most abundant benthic macrophyte in Florida Bay and is sensitive to nutrient and salinity climates. Among our study sites, the difference in total *T. testudinum* biomass did not exceed 37%. However, the threefold difference in standing crop and NPP and the link between NPP and demography are indications of the degree to which abiotic conditions can modify the role of this species in ecosystem function and habitat quality for dependant species. Aside from the obvious effects on habitat structure, increased sediment organic matter content associated with elevated productivity has the potential to create sulfate-reducing conditions that have been implicated in mollusk deaths (Ferguson 2008) and seagrass die-off in Florida Bay (Zieman et al. 1999; Koch et al. 2007b; Ruiz-Halpern et al. 2008).

Restoration plans for the Everglades include an increase in freshwater flow through the Everglades and adjacent ecosystems, which will alter salinity climates in Florida Bay and facilitate the reorganization of benthic communities. We expect that anticipated reductions in salinity and changes in the variability in salinity climate will decrease the importance of *T. testudinum* in the northern regions of the bay because of decreased growth rate and perhaps increased mortality; possibly leading to the reestablishment of the *H. wrightii*-dominated seagrass beds reported by Schmidt (1979) in the 1970s in northeastern Florida Bay. An exception may be the mangrove-lined coast where P

enrichment may be sufficient to sustain viable but salinity-stressed populations of *T. testudinum*. Under these altered abiotic conditions, *H. wrightii* and *R. maritima* will be at a competitive advantage and likely to become more common (Fourqurean et al. 2003b).

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