Sea-level rise and drought interactions accelerate forest decline on the Gulf Coast of Florida, USA

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Abstract

Sea-level rise threatens low-lying coastal ecosystems globally. In Florida, USA, salinity stress due to increased tidal flooding contributes to the dramatic and well documented decline of species-rich coastal forest areas along the Gulf of Mexico. Here, we present the results of a study of coastal forest stand dynamics in thirteen 400 m^2 plots representing an elevation gradient of 0.58–1.1 m affected by tidal flooding and rising sea levels. We extended previously published data from 1992–2000 to 2005 to quantify the full magnitude of the 1998–2002 La Niña-associated drought. Populations of the dominant tree species, *Sabal palmetto* (cabbage palm), declined more rapidly during 2000–2005 than predicted from linear regressions based on the 1992–2000 data. Dramatic increases in *Juniperus virginiana* (Southern red cedar) and *S. palmetto* mortality during 2000–2005 as compared with 1995–2000 are apparently due to the combined effects of a major drought and ongoing sea-level rise. Additionally, coastal forest stands continued to decline in species richness with increased tidal flooding frequency and decreasing elevation. Stable isotope (H, O) analyses demonstrate that *J. virginiana* accesses fresher water sources more than *S. palmetto*. Carbon isotopes reveal increasing $\delta^{13}C$ enrichment of *S. palmetto* and *J. virginiana* with increased tidal flooding and decreased elevation, demonstrating increasing water stress in both species. Coastal forests with frequent tidal flooding are unable to support species-rich forests or support regeneration of the most salt-tolerant tree species over time. Given that rates of sea-level rise are predicted to increase and periodic droughts are expected to intensify in the future due to global climate change, coastal forest communities are in jeopardy if their inland retreat is restricted.

Keywords: climate change, global warming, *Juniperus virginiana*, La Niña, *Sabal palmetto*, salt tolerance, sea-level rise, species richness, stable isotopes, tidal flooding

Received 11 November 2006; revised version received 18 May 2006 and accepted 8 June 2007

Introduction

Increased CO_2 emissions and global warming have accelerated sea-level rise due to the thermal expansion of water and glacial melting (Meier & Wahr, 2002; Meehl *et al.*, 2005). Rising seas are causing the loss of coastal forests, salt-marshes, coral reefs, and shallow marine benthic communities (Williams *et al.*, 1999, 2003; Denslow & Battaglia, 2002; Jokiel & Brown, 2004; Schiel *et al.*, 2004; Donner *et al.*, 2005; Silliman *et al.*, 2005;

Rogers *et al.*, 2006). Interactions between sea-level rise and periodic droughts are also known to expedite the loss of coastal salt marshes in North America and Australia (Silliman *et al.*, 2005; Rogers *et al.*, 2006). Coastal forests may be similarly threatened by ongoing sea-level rise and drought events (Williams *et al.*, 2003); therefore, it is imperative that we understand the synergistic interactions and quantify the changing magnitudes of these interactions over time.

The Gulf of Mexico's coastal ecosystems are seriously threatened by ongoing sea-level rise (Twilley *et al.*, 2001). Recent rates of relative sea-level rise along the Gulf of Mexico are documented as high as 11.9 mm yr^{-1}

in Louisiana (Penland & Ramsey, 1990), approximately 20 times background Holocene rates in the Mississippi delta of only 0.5–0.6 mm per year (Törnqvist & Gonzalez, 2002). Rising seas and the accompanying salt water intrusions cause reduced canopy tree regeneration, declines in overstory tree species diversity, and the eventual retreat of coastal forests along the Gulf coast (e.g. Salinas *et al.*, 1986; DeLaune *et al.*, 1987; Conner & Brody, 1989; Ross *et al.*, 1994; Williams *et al.*, 1999; Denslow & Battaglia, 2002). Florida's flat topography and low elevations render it particularly vulnerable to rapid rates of shoreline retreat (Goodbred *et al.*, 1998) and make it an excellent place to examine the effects of sea-level rise and drought on coastal forests.

Monitoring of tree populations in coastal forests in Waccasassa Bay Preserve on the Gulf of Mexico coast of Florida from 1992 through 2000 revealed failing tree regeneration and progressive tree mortality due to the chronic salt stress from sea-level rise, potentially exacerbated by storm events (Williams *et al.*, 1999, 2003). Williams *et al.* (1999) reported that sea-level rise affected forest stands first by eliminating canopy tree regeneration then by increasing the mortality rates of older trees, and eventually resulting in the replacement of forest by salt marsh. Greenhouse and field studies on the effects of salinity and tidal flooding on coastal tree species revealed that *Sabal palmetto* (cabbage palm) was the most salt-tolerant tree species, followed by *Juniperus virginiana* (Southern red cedar), *Quercus virginiana* (live oak), *Celtis laevigata* (sugarberry), and then a number of less tolerant species (Perry & Williams, 1996; Williams *et al.*, 1998). Relative salt tolerance was closely correlated with tree persistence along the elevation and tidal flooding gradient.

Understanding the declines of tree populations in coastal forests requires knowledge of species-specific salt tolerances and consequent abilities to persist in forest stands with varying degrees of access to fresh groundwater. We used stable isotope analyses to investigate uptake of fresh groundwater by *S. palmetto* and *J. virginiana*, exploring these interactions as potential causes for their declining populations in coastal forest. Previous stable isotope (hydrogen and oxygen) analyses of trees in the same study area demonstrated increasing groundwater access by *J. virginiana* with increasing elevation (Williams *et al.*, 2003). We extended this analysis to include the source water for *S. palmetto*, utilizing hydrogen and oxygen isotopes to compare *S. palmetto* and *J. virginiana* in stands along a gradient of tidal flooding frequency. Additionally, we used carbon isotopes to document differences in water stress between *S. palmetto* and *J. virginiana* across an elevation and tidal flooding gradient.

We examined changes in populations of coastal forest trees over the period of 2000–2005 to capture the full magnitude of the 1998–2002 La Niña-associated drought and to quantify the hastening effect of drought on coastal forest retreat. While Williams *et al.* (2003) documented a statistically significant increase in *J. virginiana* mortality after the 1993 'Storm of the Century,' the only increase in mortality that was detectable during the first 2 years of the 1998–2002 drought was among *J. virginiana* in the plot most frequently flooded by tides. Our objectives were to compare a period that included the latter half of the drought with earlier rates of tree mortality, recruitment and growth, as well as changes in species richness of forest stands along a gradient of declining elevation and increasing tidal flooding. We quantify the long-term synergistic effects of periodic drought and sea-level rise on coastal forest communities, which has implications for coastal ecosystem conservation and management.

Materials and methods

Study site

Waccasassa Bay Preserve State Park on the Gulf Coast of Florida (29°7′N, 82°47′W; Fig. 1) consists of tidal marshes and coastal forests that are predominantly variants of hydric hammock with some freshwater
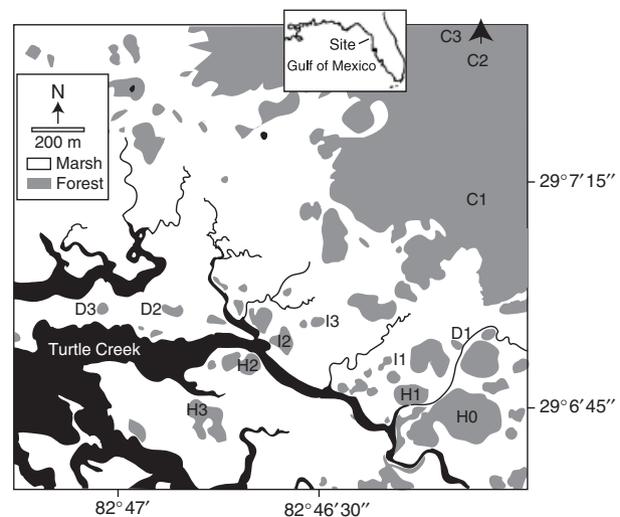

Fig. 1 Location of study plots in Waccasassa Bay Preserve on the Gulf Coast, FL, USA. Tidal creeks (black), marshes (white), and forests (gray) are illustrated. Plots were established in inland contiguous coastal forests (C1–C3) and on forest islands surrounded by tidal creeks and salt marshes of varying elevations (healthy stands, H0–H3; intermediate stands, I1–I3; and decadent stands, D1–D3). The figure was modified from Williams *et al.* (1999).

pools, basin swamps, and pine-dominated flatwoods (Abbott & Judd, 2000). Forest occurs inland as unbroken stands and closer to the coast as forest islands surrounded predominantly by *Juncus roemerianus* (black-tipped needle rush). The coastal forests within our study plots were inundated by tides at least once per week for <1–27 weeks during the 37-week census period in 1992 (hereafter referred to as weeks of flooding); flooding frequency depends on both elevation and location relative to the coast (Williams *et al.*, 1999). Plant species richness in the study area has been shown to decrease with increasing tidal flooding frequency (Williams *et al.*, 1999). While inland forests support 20–30 species of canopy trees, low-lying coastal forest stands are dominated by *S. palmetto* and *J. virginiana* but are further reduced to monodominance by *S. palmetto* at lower elevations.

Forest stand dynamics

A series of 20 m × 20 m forest plots spanning an elevation gradient were established on forested islands near the coast and in inland unbroken forest (Fig. 1). Live trees >2 m tall were identified to species, tagged, mapped, and measured within the plots annually from their establishment in 1992–1993 through 1998, and then in 2000 (Williams *et al.*, 1999, 2003). We resurveyed these plots in 2005. Heights of *S. palmetto* and the diameters at breast height (dbh) of all other trees >2 m tall were measured in 1995 and 2005. Tree regeneration was recorded by counting all trunkless *S. palmettos* and all other individual trees <2 m tall in each plot. For the plots established in 1993 and remeasured in 2005 (H0, C1–C3; Fig. 1), estimates of tree regeneration were determined with 25 evenly spaced 1 m² subplots due to the high density of tree regeneration.

Forest stand health was assessed by comparing the survivorship of *S. palmetto*, *J. virginiana*, and all other overstory taxa as a function of the frequency with which plots were inundated at least once per week and by tidal frequency categories (≥20, 10–20, 1–9, and <1 week per 37-week sampling interval, as determined by Williams *et al.*, 1999). Based on extrapolations of the 1992/1993–2000 survivorship data of *S. palmetto* and *J. virginiana* trees >2 m tall, we compared the number of trees expected to be alive with those observed alive in 2005. Average annual mortality was also determined for the most common tree species (*S. palmetto*, *J. virginiana*, *Q. virginiana*, and *C. laevigata*) and compared between 1995–2000 and 2000–2005. Height growth of *S. palmetto* and diameter growth of *J. virginiana* were calculated for 1995–2005 and plotted against tidal flooding frequency.

Rising sea levels and meteorological events

We estimate sea-level rise as the change in mean higher high water (MHHW) using NAVD88 from 1939 to 2005 in Cedar Key (NOAA: Center for Operational Oceanographic Products and Services, 2006; Fig. 2). Meteorological data including total annual precipitation from 1955 to 2005 were acquired from Tampa International Airport (Station 088788/12842, NOAA: National Climatic Data Center, 2006; Fig. 3), approximately 140 km southeast of the study area. La Niña events were taken from NOAA's Climate Prediction Center Database (2006), using the Oceanic Niño Index [3-month running mean of an ERSST.v2 SST anomalies in the Nino (5°N–5°S, 120°–170°W) regions]. These climatic and meteorological data were used to document sea-level rise and the duration and frequency of droughts.

Stable isotope analyses

Samples for the isotopic analysis of water were collected from trunk cores of *S. palmetto* and branches of *J. virginiana*. The samples (3–6 cm³ in volume) were immediately placed in sealed glass tubes to prevent evaporation. Cryogenically extracted water was decanted into vials, treated with activated carbon to remove remaining organics, and analyzed in a Finnegan Delta Plus (Finnegan, Bremen, Germany) mass spectrometer to determine oxygen and hydrogen isotope values. For assessment of water stress, samples of leaf material were collected from *S. palmetto* and *J. virginiana* for carbon isotope analysis. Leaf samples were collected, dried at 60 °C, and then homogenized and combusted using a Finnegan Delta Plus mass spectrometer to obtain carbon isotope values. All samples for isotopic analysis were collected on October 9, 2005 to avoid potentially
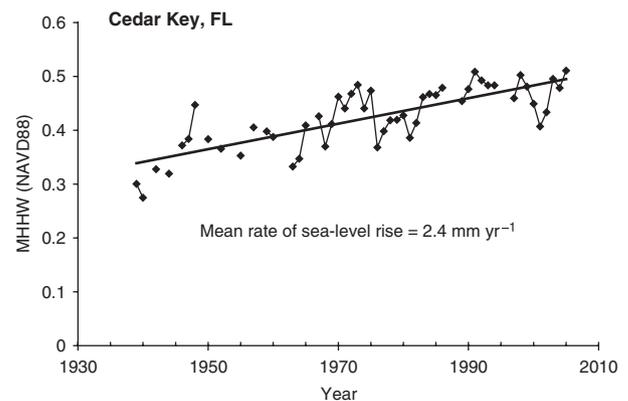

Fig. 2 Mean higher high water (MHHW) referenced to NAVD88 from 1939 to 2005 in Cedar Key, FL, USA ($y = 0.0024x - 4.252$, $r^2 = 0.61$, $\beta_{SE} = 2.6 \times 10^{-4}$). Data were acquired from NOAA at http://co-ops.nos.noaa.gov
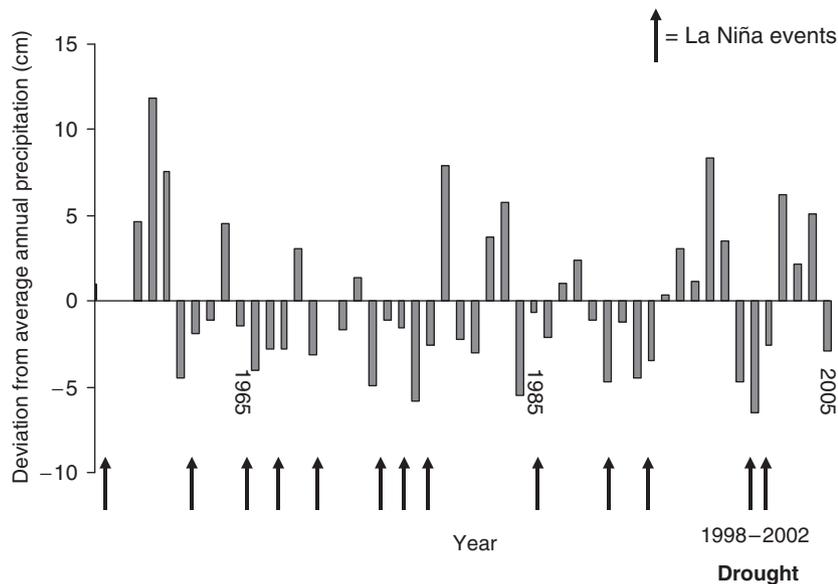
Fig. 3 Annual precipitation deviations from a 50-year average from 1955 to 2005 (Tampa International Airport; www.ncdc.noaa.com). Negative deviations indicate periods of drought; La Niña events are noted with arrows (http://www.cpc.ncep.noaa.gov/products/ analysis_monitoring/ensostuff/ensoyears.shtml).

confounding effects of temporal change in water stress; more frequently flooded plots were sampled early in the morning with healthier plots sampled as the day progressed and vapor pressure deficits increased. Samples were collected from six plots differing in elevation (0.58–0.96 m) and frequency of tidal flooding (<1–27 weeks). Additionally, water samples collected from rainfall (2 km from the study site), the site's tidal creek, a domestic well adjacent to the site (coastal aquifer), and an inland well (inland aquifer) located in Gainesville, FL (approximately 80 km from the study area) by Williams *et al.* (2003) were included for comparative purposes. One *S. palmetto* leaf sample was excluded from all analyses *post hoc* due to its anomalous $\delta^{13}C$ value (−24.3‰).

Oxygen, hydrogen, and carbon isotope values ($\delta^{18}O‰$, $\delta D‰$, and $\delta^{13}C‰$) are based on the ratios of $^{18}O/^{16}O$, D/H, and $^{13}C/^{12}C$, respectively (Coplen, 1994). The $\delta‰$ ratios are defined as: $\delta = ((R_{sample}/R_{standard}) - 1) \times 1000$, where $R = {}^{18}O/{}^{16}O$, D/H, or $^{13}C/^{12}C$ (Coplen, 1994). The water standard for oxygen and hydrogen isotope values is Standard Mean Ocean Water (V-SMOW) and the carbonate standard for carbon isotopes is Vienna Pee Dee Belemnite (V-PDB; Coplen, 1994). Accordingly, larger $\delta^{18}O$, δD, and $\delta^{13}C$ values are more enriched in ^{18}O, D, and ^{13}C than smaller values that are more depleted in ^{18}O, D, and ^{13}C, respectively. Hydrogen and oxygen isotopic analyses were run at the Stable Isotope Facility for Environmental Ratios at the University of Utah. Carbon isotope analyses were run at the Department of Geological Sciences at the University of Florida.

Results

Rising sea-levels and meteorological events

Sea-level rose in Cedar Key, approximately 30 km northwest of Waccasassa Bay, at an average rate of $2.4 \, \text{mm yr}^{-1}$ from 1939 to 2005 (NOAA: Center for Operational Oceanographic Products and Services, 2006; Fig. 2). During our study period, MHHW actually declined by approximately $3 \, \text{mm yr}^{-1}$ from 1992 to 2000 and then increased at a rate of about $17 \, \text{mm yr}^{-1}$ from 2000 to 2005 (Fig. 2).

Annual precipitation levels in Tampa from 1955 to 2005 documents numerous deviations from 50-year average levels (Fig. 3). Of particular relevance to our study was the prolonged La Niña-associated drought that occurred during 1998–2002 (Verdi *et al.*, 2006; NOAA: National Climatic Data Center, 2006; Fig. 3).

Dynamics of coastal forest decline

Coastal forest stands declined in species richness with decreasing elevation ($r^2 = 0.43$, $P < 0.05$) and increasing tidal flooding frequency ($r^2 = 0.68$, $P = 0.001$; Table 1). Before 2005, all but the most frequently flooded plot maintained populations of both *S. palmetto* and *J. virginiana*. The 2005 census documents the disappearance of *S. palmetto* > 2 m tall from the most frequently flooded plot (D2) and disappearance of *J. virginiana* from the three plots with the most frequent tidal flooding where it was present in 2000. In other words,

Table 1 Tree species presence by plot, arranged in order of increasing tidal frequency with plot elevations noted below

Tree species	Plots with tidal flooding frequency (weeks) and elevations (m)												
	C3	C1	C2	H0	H1	H3	H2	I3	I1	I2	D1	D3	D2
	<1	<1	<1	<1	1	6	8	10	13	16	18	26	27
	0.69	1.1	1.09	0.96	0.93	0.8	0.78	0.66	0.6	0.67	0.52	0.63	0.6
Sabal palmetto	R	R	R	R	R	R	R	[X]	[X]	X	X	X	[L]
Juniperus virginiana	[X]	R	[X]	R	R	[X]	[X]	X	X	[L]	[L]	[L]	–
Quercus virginiana	R	[L]	R	X	R	X	X	–	–	–	–	–	–
Quercus laurifolia	R	[L]	R	X	–	–	–	–	–	–	–	–	–
Celtis laevigata	–	X	R	–	X	X	–	–	–	–	–	–	–
Morus rubra	X	–	–	–	X	–	–	–	–	–	–	–	–
Pinus taeda	[X]	R	–	–	–	–	–	–	–	–	–	–	–
Acer floridanum	–	[L]	[X]	–	–	–	–	–	–	–	–	–	–
Ulmus alata	[X]	–	[X]	–	–	–	–	–	–	–	–	–	–
Ptelea trifoliata	–	–	R	–	–	–	–	–	–	–	–	–	–
Diospyros virginiana	R	X	–	–	–	–	–	–	–	–	–	–	–
Franxinus caroliniana	–	–	X	–	–	–	–	–	–	–	–	–	–
Gleditsia tricanthos	X	–	–	–	–	–	–	–	–	–	–	–	–

Species are listed as currently regenerating (R) or as relic stands (X), with '[X]' indicating a change from regenerating stands to relic stands 2000–2005 and '[L]' indicating the loss of a tree species present in 2000 but absent in 2005.

S. palmetto remained in plots with ≤ 26 weeks of tidal flooding, whereas *J. virginiana* was only present in plots experiencing ≤ 13 weeks of tidal flooding (Table 1). In addition to declines in species richness, regeneration of most tree species was absent from the more frequently flooded plots. Regeneration of *J. virginiana* ceased in four plots between 2000 and 2005; only three plots, all with ≤ 1 week of tidal flooding, had *J. virginiana* seedlings in 2005 (Table 1). Regeneration of *Ulmus alata* (winged elm) ceased in two inland contiguous forest plots between 2000 and 2005 while regeneration of *Pinus taeda* (loblolly pine) and *Acer floridanum* (Florida maple) each stopped in one inland forest plot (Table 1). The number of tree species apparently capable of regenerating declined with decreasing elevation ($r^2 = 0.60$, $P < 0.01$) and increasing tidal flooding frequency ($r^2 = 0.63$, $P = 0.001$; Table 1).

S. palmetto and *J. virginiana* densities in frequently flooded plots (> 8 weeks) continued to decline during 2000–2005 while their populations in less flooded plots were stable (Fig. 4). The number of surviving trees (> 2 m tall) of *S. palmetto* ($r^2 = 0.47$, $P = 0.01$) and *J. virginiana* ($r^2 = 0.58$, $P < 0.01$) declined substantially with increased tidal flooding. Additionally, increased tidal flooding frequency significantly increased mortality experienced during 2000–2005 for both *S. palmetto* ($r^2 = 0.80$, $P < 0.001$) and *J. virginiana* ($r^2 = 0.80$, $P = 0.001$). Using linear regressions of 1992–2000 tree survivorship (i.e. without considering recruitment), we predicted 2005 populations of *S. palmetto* and *J. virginiana*. The number of *S. palmetto* (> 2 m tall) observed in 2005 was significantly lower than predicted (paired Student's *t*-test: $P < 0.05$, $n = 13$); the greatest declines were in plots with ≥ 10 weeks of tidal flooding (Fig. 5). In contrast, *J. virginiana* mortality rates did not significantly differ from those predicted.

The chronic effects of sea-level rise on coastal forests in Waccasassa Bay were exacerbated by the 1998–2002 La Niña-associated drought. In particular, *S. palmetto* suffered greater mortality rates during 2000–2005 than 1995–2000 (paired Student's *t*-test: $P < 0.01$, $n = 13$; Fig. 6). Mortality rates of *S. palmetto* in plots with ≥ 8 weeks of flooding during 2000–2005 were at least two to 15 times the 1995–2000 mortality rates (Fig. 6). *J. virginiana* also suffered significantly greater (paired Student's *t*-test: $P < 0.05$, $n = 6$) mortality during 2000–2005 than during 1995–2000 in all forest plots with ≥ 1 week of flooding (Fig. 6), with mortality rates approximately 0.3–19 times greater than the earlier estimates from 1995 to 2000. In all plots where *Q. virginiana* and *C. laevigata* are present, their mortality rates did not significantly differ between 1995–2000 and 2000–2005 (Fig. 6). Recruitment of *S. palmetto* and *J. virginiana* trees into the > 2 m age class did not take place in plots with > 8 weeks of tidal flooding and only occurred at rates of < 1 tree yr^{-1} in only four plots.

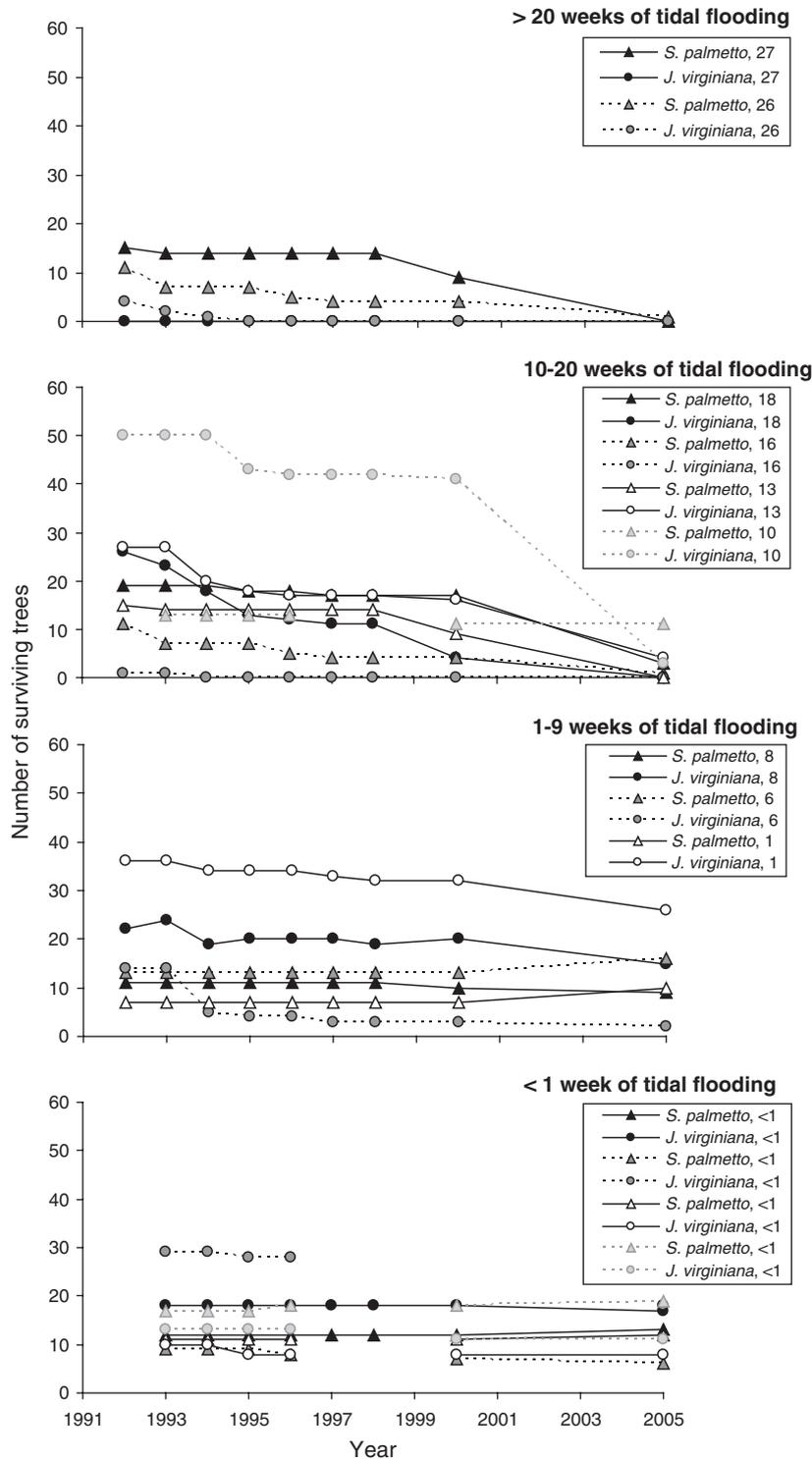Mean total height growth of *S. palmetto* during 1995–2005 declined with increasing tidal flooding frequency

Fig. 4 The number of live trees >2 m tall of *Sabal palmetto* and *Juniperus virginiana* in thirteen 20 m × 20 m plots (with weeks of tidal flooding noted), organized by number of weeks when tidal flooding is expected (>20, 10–20, 1–9, and <1 week).

($r^2 = 0.67$, $P < 0.01$; Fig. 7). Additionally, maximum growth of *S. palmetto* increased with decreasing tidal flooding ($r^2 = 0.59$, $P < 0.01$; Fig. 7). Maximum diameter growth rates of *J. virginiana* appeared to decrease with increased tidal flooding, and maximum growth rates in plots with ≥10 weeks of tidal flooding were less than half of those in inland plots (Fig. 7). However, the relationships between tidal flooding frequency and
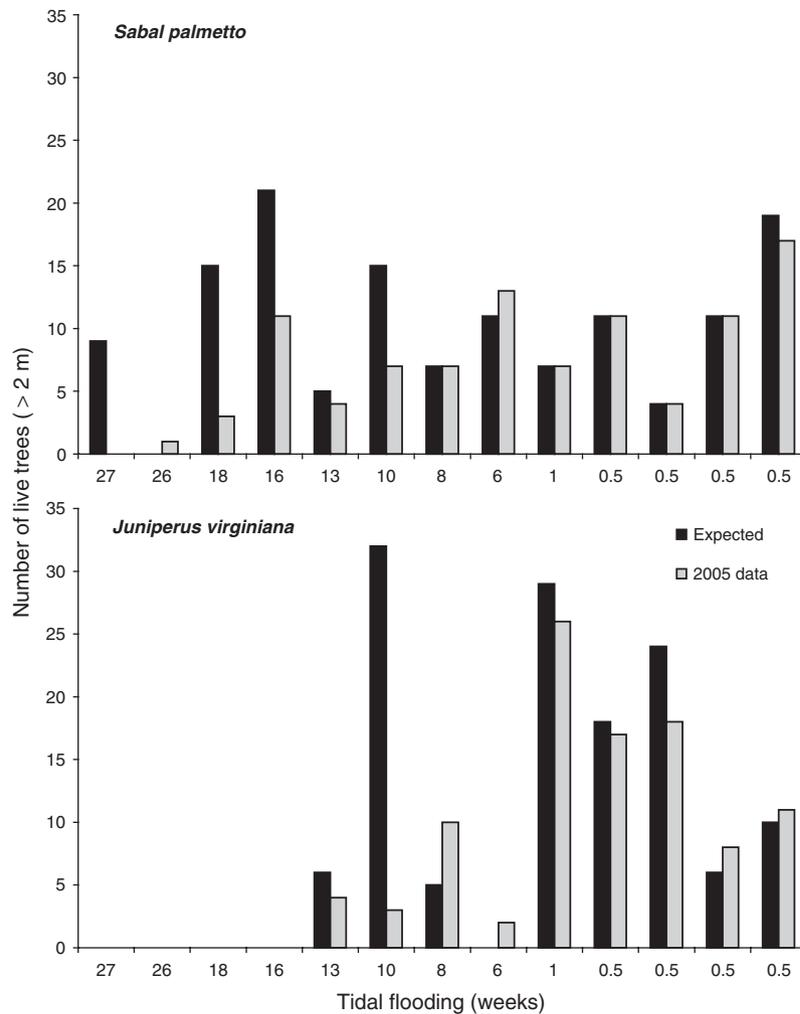
Fig. 5 Numbers of live trees >2 m tall predicted to be present in 2005 in 20 m $\times 20$ m plots subjected to different frequencies of tidal flooding. These expectations are based on the number of trees surviving from 1992 to 2000. Actual tree survivorship as observed in 2005 (gray) and expectations (black) are organized in order of declining tidal flooding frequency.

mean and maximum growth rates of *J. virginiana* were not significant (Pearson's correlations, $P = 0.79$ and 0.06, respectively).

Tree water sources and stress

δD values of *S. palmetto* were more D enriched than *J. virginiana* (mean difference $= 7.2$‰) at plots with >1 week of tidal flooding (paired Student's *t*-test: $P < 0.05$, $n = 3$; Fig. 8). Similarly, the δ^{18}O values for *S. palmetto* are more ^{18}O enriched than *J. virginiana* sampled from the same plots; these differences are nearly significant at the 0.05 level (paired Student's *t*-test: $P = 0.06$, $n = 10$; mean difference $= 1.6$‰; Fig. 8). δD and δ^{18}O values of freshwater sources (rain and aquifer) were the most negative (rain: δD $= -22$‰, δ^{18}O $= -4.3$‰; aquifer at inland and coastal sites, respectively: δD $= -28$‰, δ^{18}O $= -3.6$‰, and δD $= -23$‰, δ^{18}O $= -3.2$‰) while

tidal creek water taken near the coast was relatively D and ^{18}O enriched (δD $= -2$‰, δ^{18}O $= -0.2$‰; Williams *et al.*, 2003; Fig. 8). Source water of trees from the most frequently flooded plots is slightly but not significantly more D and ^{18}O enriched than the inland forest plot (<1 week of flooding).

Stable carbon isotopes (δ^{13}C) of *S. palmetto* and *J. virginiana* were negatively correlated with elevation ($r^2 = 0.88$, $P < 0.05$; $r^2 = 0.95$, $P = 0.026$) with slopes of -7.6 ($\beta_{SE} = 1.6$) and -12.6 ($\beta_{SE} = 2.1$), respectively (Fig. 9). δ^{13}C values of *S. palmetto* and *J. virginiana* were positively correlated with tidal flooding frequency ($r^2 = 0.87$, $P < 0.05$; $r^2 = 0.99$, $P < 0.01$) with slopes of 0.10 ($\beta_{SE} = 0.02$) and 0.36 ($\beta_{SE} = 0.03$; Fig. 9), with steeper slopes for *J. virginiana* than *S. palmetto*. These results indicate greater ^{13}C enrichment of *J. virginiana* with decreasing elevation and increasing tidal flooding frequency (Fig. 9).
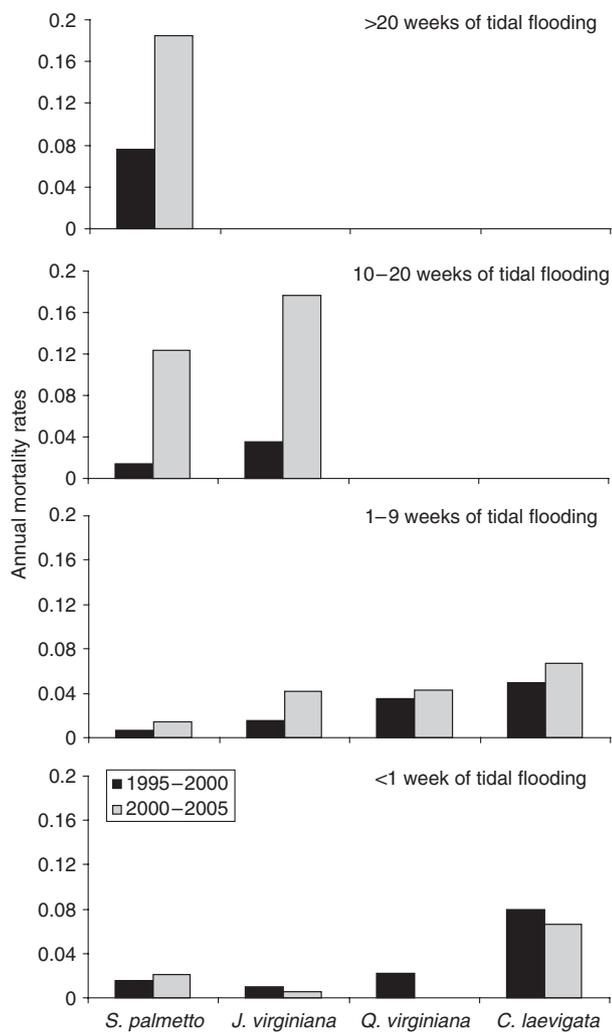
Fig. 6 Average annual mortality rates (trees yr^{-1}) for the most common tree species present (>2 m tall) in thirteen 20 m × 20 m plots. The plots are organized by tidal flooding categories, as defined in Fig. 4. Annual mortality rates are compared between two 5-year time periods, 1995–2000 (black) and 2000–2005 (gray).

Discussion

Our results indicate declines of tree populations in low-lying coastal forests beyond predictions based on population levels from just a decade ago. During the most recent (2000–2005) observation period, *S. palmetto* trees >2 m tall disappeared from the most tidally flooded plots and stopped regenerating in two plots. During this same period, *J. virginiana* disappeared from three plots and stopped regenerating in four. These dramatic changes in stand composition indicate the striking deterioration of the suitability of the sampled areas for forest. Because *J. virginiana* is less salt tolerant than *S. palmetto* (Perry & Williams, 1996; Williams *et al.*, 1998), it is likely that the high mortality rates and discontinuation of regeneration experienced by *J. virginiana*

is due to high salinity. For example, in September of 1997, groundwater conductivity ranged from 6 mS cm^{-1} (~4 g sea salt L^{-1}) in the healthiest stand to 32 mS cm^{-1} (~23 g sea salt L^{-1}) in a frequently tidally flooded forest stand in the final stages of forest loss (Williams *et al.*, 1999). Overall, the more frequently flooded plots had greater changes in species richness and regeneration status of canopy tree species than inland coastal plots. Declines in tree regeneration in the inland forest plots is likely a result of reduced precipitation as opposed to the coupled effects of drought and tidal flooding experienced by forests closer to the coast. While tree populations may continue to persist both on forest islands and inland, the lack of regeneration does not bode well for either.

Populations of *S. palmetto* declined faster than predicted from a linear extrapolation of the 1992/1993–2000 trend. Given that plots subjected to low frequencies of tidal flooding suffered only minor declines (if any) in *S. palmetto* and *J. virginiana* populations, this acceleration in mortality was disproportionately due to tree deaths in frequently flooded plots. While the La Niña-associated drought (1998–2002) intensified tree water stress across the gradient, its effect was apparently greatest in the plots most affected by sea-level rise. In other words, the drought acted like a 'knockout punch' for tree populations already suffering the effects of sea-level rise. While Williams *et al.* (2003) did not observe significant increases in mortality associated with the La Niña event during 1998–2000, the impact is obvious in our study with data spanning the entire drought period. Given that La Niña-associated droughts have occurred repeatedly in the past (NOAA: Climate Prediction Center Database, 2006) and are likely to occur at an increasing frequency in the future, coastal forest decline is likely to accelerate even if the rate of sea-level rise remains constant. Topographic variation may cause temporal variation in rates of coastal forest decline as the seas rise over flatter or more steeply sloped areas (Castaneda & Putz, 2007).

Stable hydrogen and oxygen isotopic analyses demonstrate greater δD and δ^{18}O values in *S. palmetto* than *J. virginiana*, indicating that the latter is accessing more D and ^{18}O depleted water. While *J. virginiana* may be tapping into deeper groundwater that is more D and ^{18}O depleted (Epstein & Meyeda, 1953; Cooper & DeNiro, 1989), the underlying limestone limits rooting depth. Alternatively, *J. virginiana*'s greater access to freshwater lenses may indicate greater lateral root elongation than *S. palmetto*. *J. virginiana* may instead maintain more negative δD and δ^{18}O values because they may only be able to survive to the >2 m tall age class with access to fresher (more D and ^{18}O depleted) water sources. Owing to higher salinity tolerance, *S. palmetto*
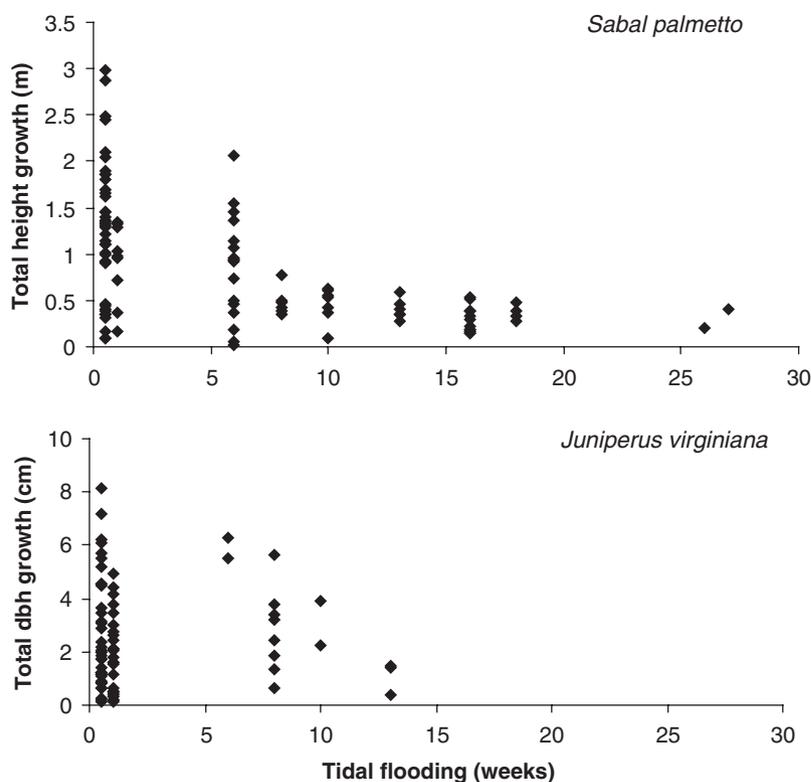
Fig. 7 Total growth of trees $\geq 2\,m$ tall between 1995 and 2005 of (a) *Sabal palmetto* (height) and (b) *Juniperus virginiana* (dbh) plotted against tidal flooding frequency (weeks with at least one episode of flooding/37 weeks sampled).
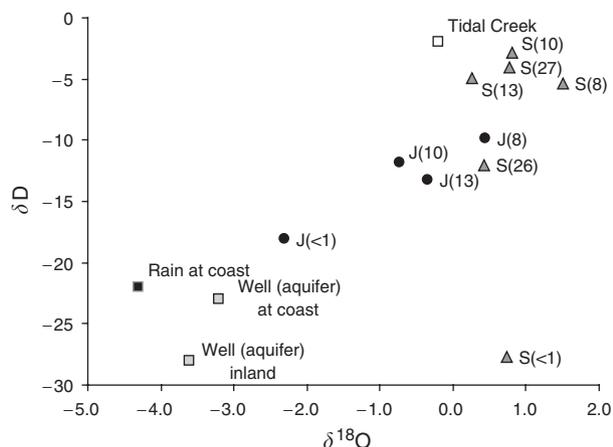

Fig. 8 Stable isotopes of xylem water in *Juniperus virginiana* (J, ●) and *Sabal palmetto* (S, △) with tidal flooding frequency (weeks/year) noted in parentheses. Water samples from the tidal creek (collected near the coast), aquifers (coastal, inland), and rainwater were taken from Williams *et al.* (2003).

persists in areas with higher salinity source water than *J. virginiana* (Perry & Williams, 1996; Williams *et al.*, 1998). Because *S. palmetto* and *J. virginiana* are more salt tolerant than other forest tree species (Williams *et al.*, 1998), they are able to persist and dominate at sites with higher salinities. Although *S. palmetto* and *J. virginiana* do suffer salt damage, they may actually benefit from the presence of moderately saline source water if competition with less salt-tolerant species is, therefore, reduced, as suggested for the interactions between mangroves and fast-growing glycophilic plants (Sternberg & Swart, 1987). Above the salinity threshold at which regeneration of *J. virginiana* ceases, *S. palmetto* maintains monodominant stands that eventually die off as the salinity continues to increase. *J. roemerianus* is usually not present within the tree islands, but it surrounds most of them. Increased tidal inundation due to rising sea levels will continue to threaten these tree communities, as reported for tropical hardwood hammocks and pine forest in the Florida Keys (Ish-Shalom *et al.*, 1992; Ross *et al.*, 1994).

Stable carbon isotopes in leaf tissue of *S. palmetto* and *J. virginiana* become more ^{13}C enriched with decreasing elevation and increasing tidal flooding frequency, indicating increasing drought stress and the need for osmotic adjustment (Ball & Farquhar, 1984; Farquhar & Richards, 1984; Ehleringer & Monson, 1993). This enrichment is potentially due to increasing saline water inputs from lower elevation plots that experience more frequent tidal flooding. ^{13}C enrichment indicates water stress that could be due to limited access to rainwater
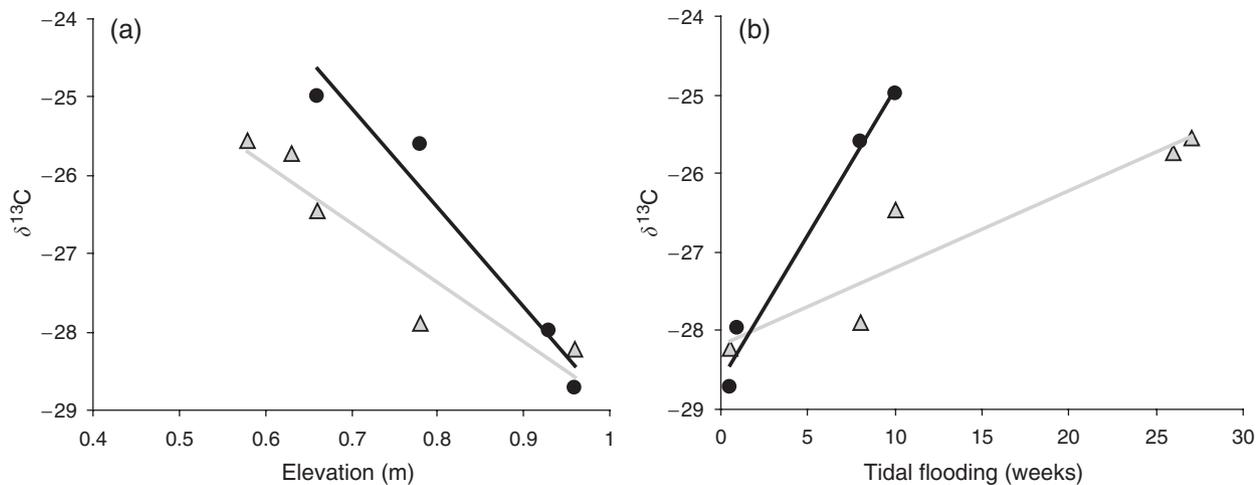
Fig. 9 Stable carbon isotopes of *Sabal palmetto* (△) and *Juniperus virginiana* (●) vs. elevation (a) and tidal flooding frequency (b). R^2 values range from 0.87 to 0.99 for all regressions plotted.

and fresh groundwater, as well as to lower canopy density (Ball & Farquhar, 1984; Farquhar & Richards, 1984; Ehleringer & Monson, 1993; Ross *et al.*, 1994; van der Merwe & Medina, 1989). The steeper slopes of increasing $\delta^{13}C$ values with decreasing elevation and increasing tidal flooding indicates greater water stress in *J. virginiana* than *S. palmetto*. Higher water stress in *J. virginiana*, which presumably results from increasing salt-water exposure and drought, contributes to its elimination at the coastal margin and to the development of monodominant *S. palmetto* stands.

Field and laboratory studies confirm that salt exposure and salinity tolerance in coastal ecosystems can be used to predict tree species presence and the failure of tree regeneration (Perry & Williams, 1996; Williams *et al.*, 1998, 1999; Thomson *et al.*, 2002; Willis & Jester, 2004). These predictions can be improved by the inclusion of the drought effect (Thomson *et al.*, 2002; Williams *et al.*, 2003), as made apparent by our 2000–2005 data. In addition to the dramatic declines in coastal forests experienced in Waccasassa Bay, extreme droughts also cause salinity levels to increase beyond tolerance levels of occupying flora elsewhere along the Gulf Coast of Mexico and in the Florida Keys (Ross *et al.*, 1994; Twilley *et al.*, 2001; Thomson *et al.*, 2002). Future drought events and ongoing sea-level rise will likely accelerate coastal forest decline along the Gulf of Mexico.

Predictions of coastal forest decline in Waccasassa Bay based on remote sensing models yield 50% decline estimates for the forests by 2093–2123 and the complete disappearance of forest stands within the preserve by 2273–2393 (Castaneda & Putz, 2007). Unfortunately, forest species are restricted in their upland migration by residential and agricultural development. It is there-fore imperative that we learn from examples like this one and make environmental policy decisions that allow for coastal forest migration. For example, lands that might support new tidal ecosystems need to be maintained as viable ecosystems that lack development, thus providing future opportunities for tidal systems to migrate inland (Pearsall, 2005). It is also necessary to consider the synergistic effects of sea-level rise and periodic droughts on coastal communities when managing coastal ecosystem (Silliman *et al.*, 2005).

Conclusion

Coastal forests in Waccasassa Bay declined during 2000–2005 at rates greater than expected from rates during the previous 8 years likely due to the synergistic effects of a drought event and sea-level rise. Tree species richness and regeneration declined with increasing tidal flooding frequency. Although the less salt-tolerant *J. virginiana* is present in lower densities than *S. palmetto* and is no longer present in the most frequently flooded plots, even *S. palmetto* (the most salt-tolerant tree species present) suffered greater than expected declines during 2000–2005. Differences in the ability of *S. palmetto* and *J. virginiana* to persist in frequently flooded plots are likely attributable to physiological differences related to salt tolerance but also due to their access to different sources of water. As suggested by Michener *et al.* (1997), we believe that the combined use of a space-for-time substitution (through the use of tidal flooding and elevation gradients) and long-term monitoring provides an effective method for quantifying the impacts of meteorological events and rising seas on coastal communities. With expected increases in the rate of sea-level rise coupled with increasing drought frequencies

due to global climate change, accelerated rates of coastal forests disappearance are likely and may already be evident.

Acknowledgements

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