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Clara Chaisson
Connecticut College, cchaisso@conncoll.edu

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Factors Influencing Stem Density of Creekbank *Spartina alterniflora* in a New England Salt Marsh

Clara Chaisson

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of
Bachelor of Arts in Botany

Members of Honors Committee

Thesis Advisor: Dr. Chad Jones, Assistant Professor of Botany and Environmental Studies

Second Reader: Dr. R. Scott Warren, Jean C. Tempel '65 Professor Emeritus of Botany

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Abstract

Stem density patterns for smooth cordgrass, *Spartina alterniflora,* are highly variable both among years and within the growing season. These variations can have consequences for the overall primary productivity of the salt marsh system, as well as its ability to provide essential ecosystem functions. In this study, I explored factors that could be driving observed variations in four tidal creeks of the Plum Island Sound Estuary, Massachusetts. End of season stem densities were measured at two of the creeks over eight years. Seasonal stem densities were measured at all four of the creeks four times during a single growing season. My objectives were to assess the influence of temperature, precipitation, tide level, and solar radiation on stem density variations among years, and to determine whether seasonal loss of stems was due to self-thinning or tidal action. Years with higher precipitation were associated with higher densities ($p = 0.001$), which may be due to an alleviation of salt stress in those years. Patterns of seasonal stem loss were more consistent with patterns of self-thinning, which has not been previously considered for *S. alterniflora*, than tidal action, which has been the predominant assumption. However, self-thinning and tidal action may be working in conjunction to cause seasonal stem loss. These results increase our ability to estimate *S. alterniflora* productivity, and our understanding of the species' ecology and its responses to current and future climatological events.

Introduction

An estimated 40% of the world's population lives within 100km of the coast (Martinez et al 2011). As a result, coastal ecosystems are some of the most threatened in the world; globally, 50% of salt marshes have either been lost or degraded (Barbier et al 2011). The incentive to conserve remaining salt marshes is substantial because salt marshes can provide a number of important ecosystem services to humans inhabiting nearby areas. These include erosion control, flood prevention, and water purification (Barbier et al 2011, Charles and Dukes 2009, Shepard, Crain, and Beck 2011).

Marsh vegetation can reduce erosion to shorelines by both trapping sediment and reducing the friction and height of waves (Barbier et al 2011). Salt marsh wave attenuation also protects coastlines from flooding and surges caused by storms and hurricanes (Barbier et al 2011, Shepard, Crain, and Beck 2011). Interest in this particular ability of salt marshes was peaked after Hurricane Katrina in 2005, when extensive damage from storm surges was blamed in part on regional marsh loss (Shepard, Crain, and Beck 2011).

Salt marshes are able to improve water quality through a process of natural filtration. Groundwater, runoff, and river water that flows through marshes is slowed by salt marsh grasses, which subsequently take up many of the nutrients contained within (Barbier et al 2011). This process is important for the health of both nearby ecosystems and humans.

Salt marshes are also among the most productive ecosystems in the world, on a comparable level with tropical rainforests and coral reefs (Johnson and Jessen 2008). The ecosystem services provided by these systems are highly dependent on productivity, meaning that accurate assessments of primary productivity are crucial for assessing their ecological functioning (Charles and Dukes 2009, Shepard, Crain, and Beck 2011). Shepard et al (2011) found that the vegetation on the marsh edge has the most significant effect on wave attenuation. As such, identifying the factors and interactions that affect primary productivity for species that are found in these areas of the marsh is important.

In New England salt marshes, the low marsh zone is almost exclusively characterized by pure stands of the grass *Spartina alterniflora.* The productivity of *S. alterniflora* can vary widely between different systems (Kirwan et al 2009), as well as among years in the same systems (Morris and Haskin 1990). Temperature and sea level have been shown to affect *S. alterniflora* productivity (Charles and Dukes 2009, Kirwan et al 2009, Warren and Niering 1993), and precipitation and solar radiation are hypothesized to have impacts as well (Kirwan et al 2009). Kirwan et al (2009) found a strong latitudinal gradient in *S. alterniflora* productivity, suggesting the importance of climate in regulating production. However, they also reported that the inter-annual variability within a local system could approach the variability observed across the entire latitudinal gradient, from the Canadian Maritimes to the Gulf of Mexico. The system-wide factors that drive and regulate annual variation at local sites are poorly understood.

Additionally, *S. alterniflora* productivity varies within the growing season. Throughout the growing season, entire *S. alterniflora* shoots can be lost, particularly after June when peak stem density is reached (Cranford et al 1989). It has been widely noted that seasonal productivity of *S. alterniflora* is often underestimated due to a failure to incorporate this export and loss into calculations, due in part to the difficulty of quantifying it (Cranford et al 1989, Dickeman, Stewart, and Wetzel 1986, Silliman and Bartolus 2003, Silliman and Zieman 2001). Due to *S. alterniflora*'s daily exposure to tidal action, Cranford et al (1989) explored tidal action as a mechanism for loss. Whether or not it is directly responsible for the loss, tidal action does make it difficult to quantify as ebbing tides quickly export lost shoots out of the system.

Alternatively, self-thinning could lead to this loss of stems over the growing season. Self-thinning has been shown to occur due to competition amongst individuals in monocultures (Ellison 1987), particularly in forest stands (Zeide 2010). *S. alterniflora* occurs in dense monocultures in the low marsh; however, the possibility of self-thinning as an explanation for *S. alterniflora* loss has largely been unexamined.

If tidal action is responsible for seasonal *S. alterniflora* stem loss, an inverse correlation between elevation and degree of loss would be expected. Shoots at lower elevations would presumably be exposed to more rigorous tidal action, and thus would undergo a greater degree of loss. This is indeed the relationship that Cranford et al (1989) observed. Additionally, if tidal action is responsible for *S. alterniflora* stem loss, relative position within the system would presumably influence rate of loss, with areas closest to the source of the incoming tide undergoing greater loss.

If self-thinning is responsible for seasonal *S. alterniflora* stem loss, areas with higher initial stem densities would presumably undergo greater stem loss, due to greater competition between individual culms. In addition, several previous studies have found that self-thinning systems have decreasing skewness in height distributions over time due to the death of smaller plants (Shibuya et al 2004, Xue and Hagihara 1999), although others have observed self-thinning without this pattern (Knox et al 1989). There is a well-established negative correlation between plant biomass and stem density in systems that self-thin (deKroon and Kalliola 1994, Lonsdale and Watkinson 1983, Shibuya et al 2004, Xue and Hagihara 1999, Xue et al 2010); this pattern would also be expected if self-thinning is operating in this system.

My study focused specifically on factors driving *S. alterniflora* stem density, a component of productivity that has not been the primary focus of previous studies on *S. alterniflora*. Primary productivity is typically expressed as dry weight per unit area per unit time, and is thus impacted by temporal changes in stem density. Additionally, stem density has been shown to have a significant effect on the ability of marshes to provide essential services such as wave attenuation and shore stabilization, meaning that temporal variations in density could correspond with temporal variations in service provision (Charles and Dukes 2009, Shepard, Crain, and Beck 2011). My goal in this investigation was to determine the influence of temperature, precipitation, tide level, and solar radiation on stem density among years, and whether seasonal loss of stems is due primarily to tidal action or self-thinning.

A more complete understanding of the factors that contribute to variations in *S. alterniflora* stem densities both within the growing season and between years will inform our understanding of the species' ecology, improve our ability to calculate accurate estimates of annual and seasonal primary productivity, and develop our understanding of which temporal variations influence salt marsh ecosystem services, impacting how they will respond to current and future climatological events.

Methods

Site Description

The study was conducted within the extensive Plum Island Sound estuary in northeastern Massachusetts, which encompasses the largest expanse of intertidal marsh in the Northeast, ca. 40,000 ha (http://ecosystems.mbl.edu/pie/site.html), and includes the Ipswich, Parker, and Rowley Rivers (Figure 1). The Plum Island Sound marshes are typical of a New England salt marsh, with distinct patterns of vegetation zonation; the low marsh, directly adjacent to the creek bank and flooded daily, is characterized by a monoculture of tall-form *S. alterniflora*, while the high marsh, approximately between MHW and extreme spring HW, is dominated by the less flood-tolerant *S. patens,* often mixed with varying amounts of *Distichlis spicata,* and interspersed with stands of short-form *S. alterniflora.* Other species such as *Juncus gerardii, Triglochin maritima,* and the annuals *Salicornia europea* and *Suaeda maritima* are also present in the high marsh.

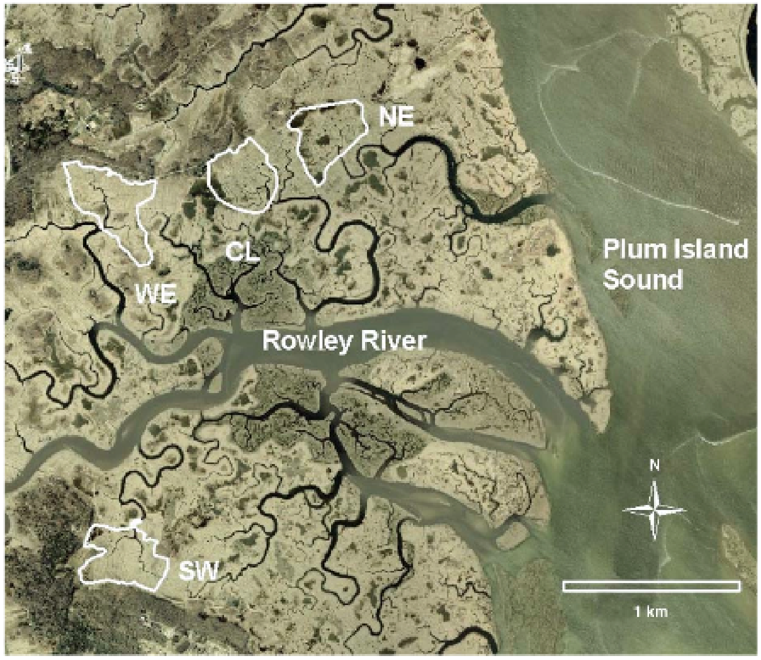

Figure 1. The Rowley River and associated tidal salt marsh creeks. Study creeks (Sweeney - SW, West - WE, Nelson - NE, Clubhead - CL) are outlined in white. Photograph is from Deegan et al 2007.

The study site included four tidal creeks (Sweeney, West, Nelson, and Clubhead) of the Rowley River in Rowley and Ipswich, Massachusetts. The site is also the focus of the Trophic cascades and Interacting control processes in a Detritus-based aquatic Ecosystem (TIDE) project, an ongoing study centered at the Marine Biological Laboratory (http://new-www.mbl.edu/tide/). One principal goal of TIDE is to determine the long-term effects of anthropogenic eutrophication on coastal marshes; two of the four study creeks, Sweeney and Clubhead, are experimentally manipulated with nitrogen fertilizer, and the other two creeks, West and Nelson, serve as references (Deegan et al 2007). Sweeney Creek has been fertilized since 2004, while Clubhead has been fertilized since 2008. Nitrate is pumped into the fertilized creeks on the incoming high tide to reach a target concentration of 70µM, 10-15x the background levels (Deegan et al 2007, Drake et al 2009).

Each of the four study creeks has two branches; for the purpose of the experiment, both branches were studied in Sweeney and West, while in Clubhead and Nelson, only one branch of each was studied, for a total of six branches. At each of the six branches, three points along the creek bank that supported pure stands of tall form *S. alterniflora* were established and marked with colored poles. Starting from the confluence, the points were spaced approximately 50-70 m from each other and numbered 1-3, with #1 corresponding to the point that was most proximate to the creek's confluence. These same points have been used as the designated *S. alterniflora* sampling locations from 2003 to 2011.

Inter-Annual Measurements

S. alterniflora stem densities were measured at each of the six points for Sweeney (fertilized) and West (reference) creeks every year from 2003 to 2011. Measurements were taken in August, near the end of the growing season. To obtain stem densities, four 0.25 m^2 quadrats were placed haphazardly within 10m of each of the three points within the tall *S. alterniflora* zone; every *S. alterniflora* stem within each quadrat was counted. Quadrat densities were averaged (N = 12 $year^{-1}$ $creek^{-1}$) for each creek for each year.

Seasonal Measurements

Seasonal measurements of *S. alterniflora* were conducted four times throughout the 2011 growing season (June 14-23, July 11-14, August 17-25, and September 12-15). Stem densities were measured using the same procedure as for the end of season measurements, but for each of the four creeks; four 0.25 m^2 quadrats were placed haphazardly near each of the eighteen colored poles, and *S. alterniflora* stem densities were sampled with the end-of-season protocol described above. To obtain an adequate sampling of the range of stem heights in each quadrat, all of the stems from one quarter of each quadrat were cut from the ground and taken back to the lab. Each harvested shoot was measured for height from the bottom of the stem to the end of the longest leaf. To ensure that stem densities were not counted in areas that had been previously cut, the quadrats were placed in slightly different locations each month. In June, the quadrats were placed starting from 1m to the right of the colored poles, in July, starting from 1m to their left, and in August, the quadrats were placed directly in front of the colored poles.

In September, quadrats were placed in all three areas at random; points that appeared to have been previously cut were avoided. The average density among the four quadrats was calculated at each point in each month and used for analysis.

Data Analysis – Inter-Annual Variation

I analyzed the effect of several environmental factors on the yearly average densities of *S. alterniflora* from 2003-2011. Creek (Sweeney [fertilized] vs. West [reference]) was also included as an independent variable. The environmental factors included: growing season (June-September) precipitation (mm), average growing season mean high water (MHW), growing season solar radiation (Watts m^{-2}), and growing degree days (GDD), which was calculated using a base temperature of 0°C.

I obtained the majority of the environmental factor data from the Plum Island Ecosystems Long Term Ecological Research (PIE-LTER) Weather Station. Between April 2001 and July 2007, the station was located on the Governor Dummer Academy campus in Byfield, MA; after July 2007, the station was moved to the Marine Biological Laboratory Marshview Farm Field Station in Newbury, MA, approximately 2 miles away. The weather station takes measurements every 15 minutes; I used daily averages of these measurements. The MHW values were from the National Oceanic and Atmospheric Administration's (NOAA's) Boston station. The station is located approximately 35 miles southwest of the study site, and was the nearest station with a complete data set from 2003 to 2011.

I assessed the cumulative effect of the environmental factors on average density for each creek for each year using a multiple regression, which was calculated in SPSS Version 19 (IBM Corporation, Armonk, NY, USA).

Data Analysis – Seasonal Variation

The data collected during the 2011 growing season were analyzed in order to determine whether the observed seasonal changes in density were due to self-thinning, or tidal action. Again, I used SPSS to calculate a multiple regression. The independent variables were fertilization treatment (whether or not a given creek had been receiving fertilization treatments via the TIDE project), position within the creekshed (as two dichotomous variables for point 1 and 2), initial density, and elevation. The dependent variable was percent loss, which was calculated as the proportion of the initial stem density (sampled in June) that was lost between June and September. Before performing the multiple regression, I tested all variables for normality using a Shapiro-Wilks test in SPSS. Only elevation showed a significant lack of normality; I used an inverse square transformation to normalize the elevation data before performing the multiple regression.

I calculated the Pearson correlations between the average stem heights and the average stem densities of each creek in SPSS. I measured the skewness in the distribution of stem heights in June and September at each point and compared skewness at the two dates for each creek using paired samples t-tests in SPSS.

Results

Inter-Annual Variation

Average stem density varied considerably among years in both Sweeney and West creeks (Figure 2). Both creeks followed a similar general pattern of change, but West had consistently higher densities. The magnitude of the differences did not seem to change with time, despite the initiation of fertilizer treatments in Sweeney in 2004.

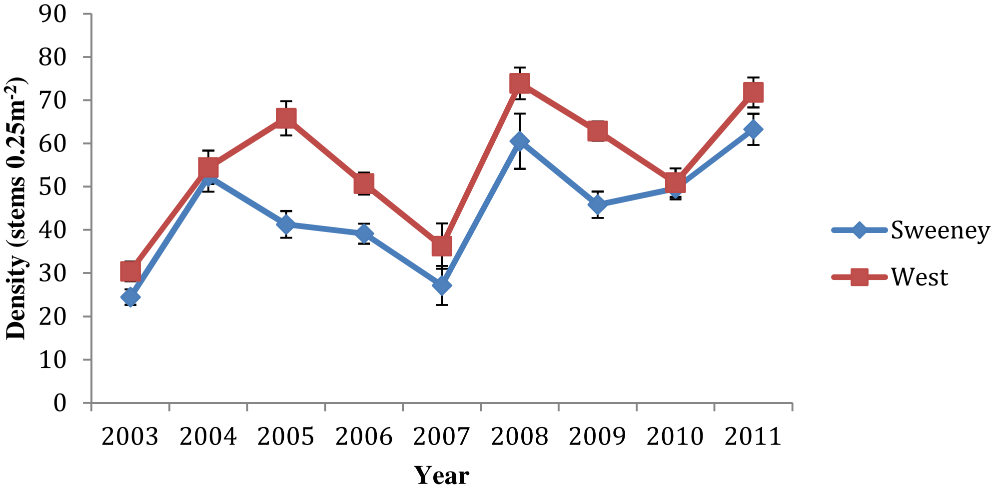

Figure 2. Changes in creek-bank *S. alterniflora* stem density in Sweeney (fertilized) and West (reference) creeks from 2003 to 2011. Error bars represent Standard Error.

Total growing season rainfall was widely variable among the years between 2003 and 2011 (Figure 3a). Average growing season MHW increased steadily from a starting point at 3.05m in 2003, to 3.17m in 2011 (Figure 3b). Growing degree days initially underwent a sloping increase until a peak in 2006, when it began decreasing until 2009, and peaked again in 2010 (Figure 3c). Average growing season solar radiation was widely variable amongst the years (Figure 3d)

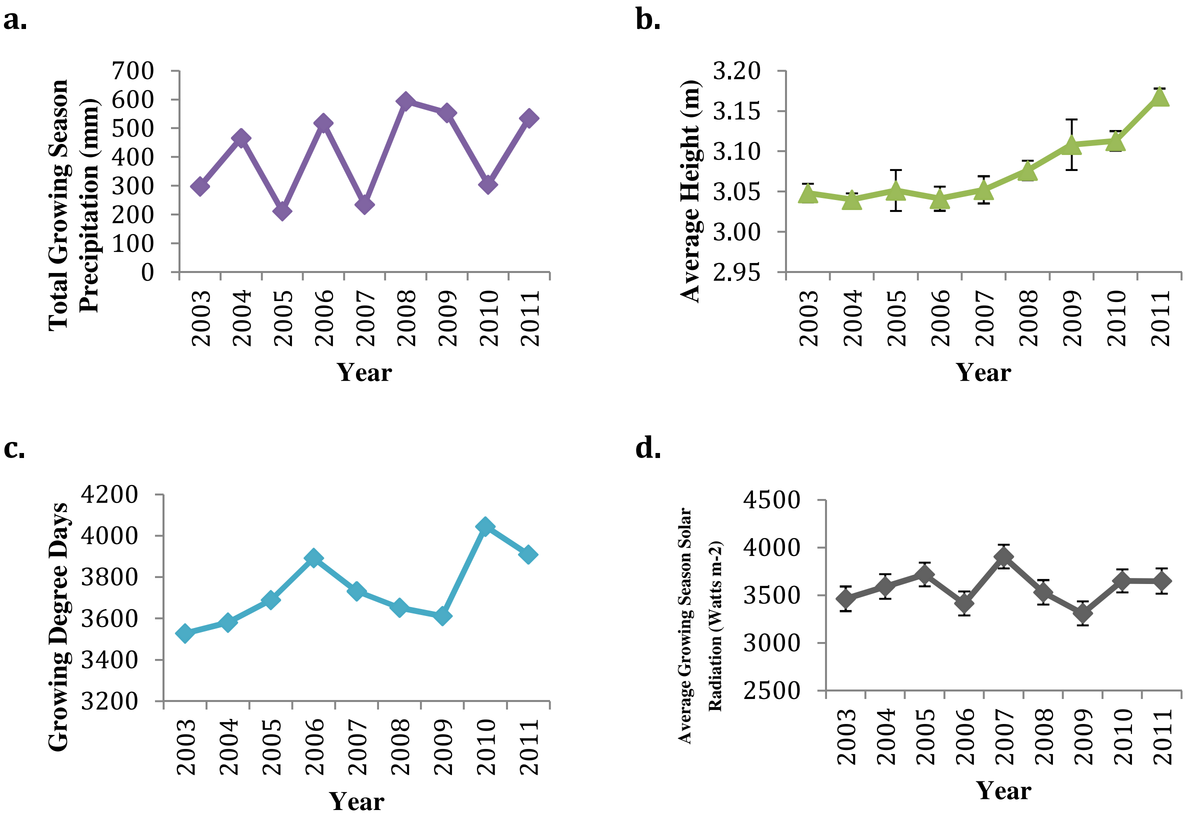

Figure 3. **a.** Changes in total growing season precipitation in Byfield, MA and Newbury, MA from 2003 to 2011. **b.** Changes in average growing season mean high water (relative to Mean Lower Low Water (MLLW)) in Boston, MA from 2003 to 2011. Error bars represent Standard Error. **c.** Changes in growing degree days in Byfield, MA and Newbury, MA from 2003 to 2011. **d.** Changes in average growing season solar radiation in Byfield, MA and Newbury, MA from 2003 to 2011. Error bars represent Standard Error.

The environmental factors assessed explain 49% of the variability in inter-annual stem density averages in Sweeney and West creeks (Table 1). Average stem density was higher in years with higher growing season precipitation (p = 0.018). Average stem density was higher in West creek, but not quite significantly (p = 0.059). Mean high water, growing degree days, and solar radiation did not have a significant effect on stem density.

Table 1. Multiple regression results showing the combined effect of creek (Sweeney vs. West), total growing season precipitation, average growing season mean high water, average growing season solar radiation, and growing degree days on average yearly stem density of *S. alterniflora*.

Overall Model	
Adjusted R Square	0.491
F	4.281
p	0.018

Independent Variables

Variable	B Coefficient	p
Creek	-10.401	0.059
Precipitation	0.07	0.018
MHW	103.884	0.205
Solar Radiation	0.028	0.198
GDD	-0.001	0.960

Seasonal Variation

Average stem density declined over the growing season in all four creeks (Figure 4). Nelson's greatest stem loss occurred between July and August, while in the other three creeks, the greatest stem loss occurred between June and July. As average stem densities decreased throughout the growing season, average stem height increased, peaking in August (Figure 5). The negative correlation between stem density and stem height was strong in Sweeney and West creeks (-0.95 and -0.94), relatively strong in Nelson (-0.86), and not as strong in Clubhead (-0.59).

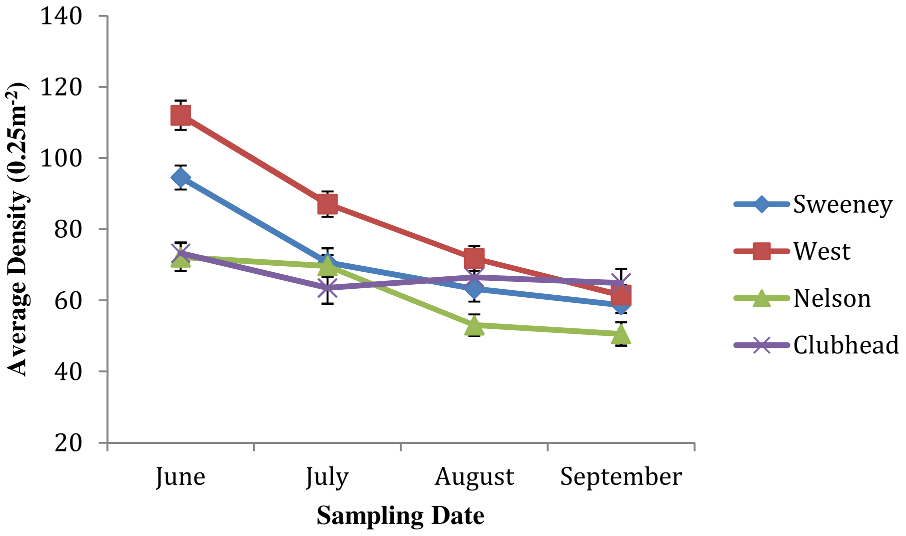

Figure 4. Changes in average *S. alterniflora* stem density in Sweeney (fertilized), West (reference), Nelson (reference), and Clubhead (fertilized) creeks from June through September 2011. Error bars represent Standard Error.

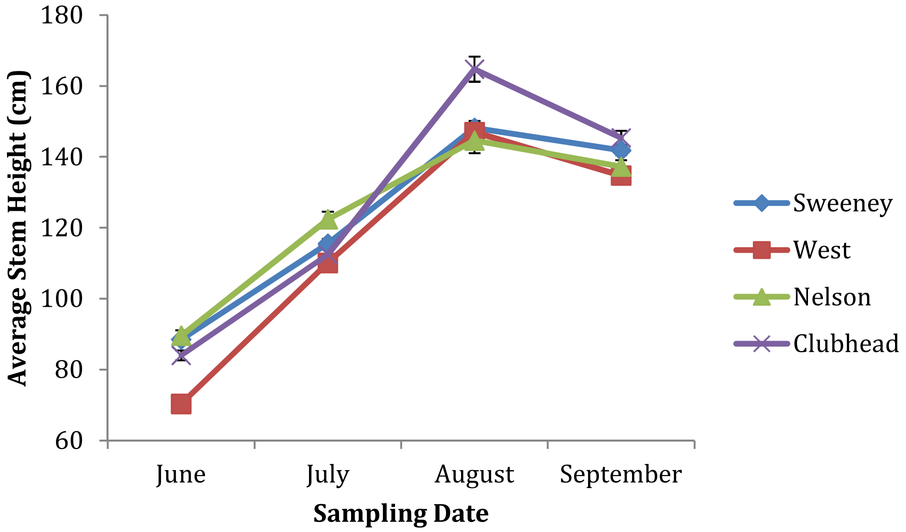

Figure 5. Changes in average *S. alterniflora* stem height in Sweeney (fertilized), West (reference), Nelson (reference), and Clubhead (fertilized) creeks from June through September 2011. Error bars represent Standard Error.

The model was able to explain approximately 58% of the variation in the loss of stems over the course of the growing season (Table 3). Points with higher initial density had higher percent loss ($p = 0.001$). Points farthest downstream (Position 1) had lower loss than those farthest upstream, but not quite significantly (p = 0.055). Fertilization and elevation did not have significant effects on percent loss.

Table 3. Multiple Regression results showing the effect of fertilizer treatment, initial density, proximity to the confluence, and elevation on percent loss of *S. alterniflora* stem density between June and September 2011.

Overall Model

Adjusted R Square	0.577
F	5.630
p	0.007

Independent Variables

Variable	**B Coefficient**	**p**
+ Fertilizer	-6.576	0.215
Initial Density	0.523	0.001
Point 1 (downstream)	-12.974	0.055
Point 2 (intermediate)	-4.647	0.407
Elevation	18.063	0.338

Skewness in stem height distribution decreased between June and September for all creeks, but not significantly (p > 0.105; Figure 6).

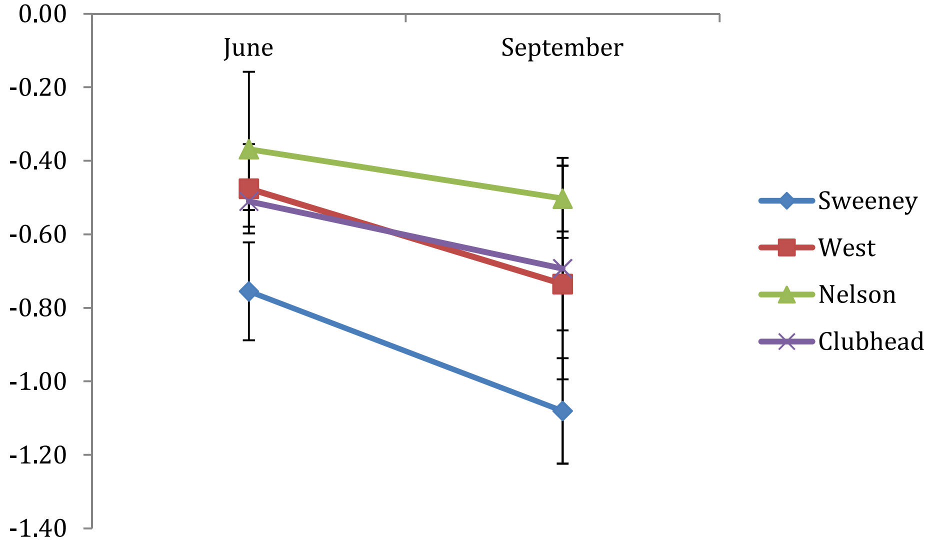

Figure 6. Changes in skewness in height distribution in Sweeney, West, Nelson, and Clubhead creeks between June and September 2011. Error bars represent Standard Error.

Discussion

Inter-Annual Variation

My results indicate that *S. alterniflora* stem densities are higher in years with higher growing season precipitation. A possible explanation for this relationship is that salinity is lowered in the system in years with high precipitation. Crain et al (2004) found that *S. alterniflora* actually performs better in fresh water than salt water, and is only found in monocultures in the low salt marsh because elsewhere it is outcompeted by other species. If this is the case, then the growth of *S. alterniflora* might increase in years when it faces less salt stress due to lower salinity from increased precipitation. To verify this hypothesis, more research is needed in order to determine whether or not salinity in the system is significantly reduced in years with higher precipitation. Depending on how climate change shifts patterns of precipitation, *S. alterniflora* density in this system may either increase or decrease in response.

The independent variables used in the model only explain half of the variation in average *S. alterniflora* stem density among years. It is evident from the results that other unmeasured factors are also influencing *S. alterniflora* stem density in this system. Kirwan et al (2009) suggested salinity, elevation, herbivory, and nutrient availability as possible local influences on productivity. Future studies should further explore the relationship between these factors and *S. alterniflora* stem density.

My results also indicate that stem densities are higher in West creek. Although this second finding is not quite significant, it suggests that variability exists even within systems at the creek level, an idea supported by Kirwan et al (2009), who noted instances of significant variability in *S. alterniflora* within single study sites in their review of salt marsh productivity. The most apparent variable between these two creeks is fertilizer treatment; Sweeney creek has been fertilized since 2004, West is a reference creek. Fertilizer treatment may be responsible for differences in *S. alterniflora* productivity between these two creeks, a hypothesis that the TIDE project is actively investigating.

Seasonal Variation

Seasonal stem loss in these creeks was substantial, ranging from 10% to 60% at the different sampling points. These results underscore the importance of the effect that seasonal stem loss has on productivity measurements and the dynamics of the system.

Patterns of stem loss are more consistent with loss of stems due to self-thinning than with tidal action. The independent variables used in the model explain 58% of the variation in seasonal loss of *S. alterniflora* stems. The initial density of the sample site was associated with higher rates of loss; these findings are consistent with the patterns predicted for a system undergoing self-thinning (deKroon and Kalliola 1995, Ellison 1987). Elevation, which would presumably be negatively correlated with loss in a system whose loss was driven by tidal action (Cranford et al 1989), was not significant. Upstream sampling locations tended to have lower rates of stem loss, which is the opposite of the expected pattern for loss associated with tidal action.

As stem density decreased over the growing season, plant height increased. Self-thinning systems have a well-established pattern of increasing plant biomass with decreasing stem density (deKroon and Kalliola 1994, Lonsdale and Watkinson 1983, Shibuya et al 2004, Xue and Hagihara 1999, Xue et al 2010). As plant height is one factor used to calculate plant biomass, this relationship may suggest more evidence for self-thinning in this system.

Skewness in stem height distribution did decrease over the growing season, but was highly variable among points. Although decreases in height skewness are often noted in self-thinning systems, Knox et al (1989) observed self-thinning in loblolly pine stands without significant decreases in height skewness over time. This suggests that skewness patterns as related to self-thinning may be dynamic depending on the species involved. The fact that decreasing height skewness in this system was not significant does not conclusively determine whether or not the seasonal loss in *S. alterniflora* stem density in this system is due to self-thinning.

Self-thinning has not been previously used to describe seasonal *S. alterniflora* stem loss, nor has it been tested as a mechanism for loss. This may be due to the common assumption that clonal plants do not self-thin (deKroon and Kalliola 1995). However, deKroon and Kalliola (1995) found that evidence for this assumption is lacking, and that changes over time in the population structure of the rhizomatous grass *Gynerium sagittatum* are entirely consistent with patterns of self-thinning observed in other species. The results of this study suggest that seasonal stem loss of *S. alterniflora* may be due in part to self-thinning. As other grasses can and do self-thin, this process should be further explored for *S. alterniflora*.

Previous studies have attempted to quantify seasonal loss without explaining its cause (Dickeman, Stewart, and Wetzel 1986). Cranford et al (1989) found that stem loss increased as elevation decreased, a trend that was not evident in this study. However, they compared export from 3 different elevations with an overall difference of 2.5m between sampling sites. The differences in elevations in the system that I studied were smaller; the elevations of each sampling site all fell within 40cm of each other. Thus, tidal action may have been responsible for some of the stem loss observed throughout the growing season, but it is difficult to quantify because of the modest variation in elevation. Further research in a site with more variable elevation may be able to explore the relationship and combined effects of self-thinning and elevation. Presumably the two are not mutually exclusive, and could be operating simultaneously, with relative importance varying with location within the system as well as between systems. Additionally, even if self-thinning is primarily responsible for seasonal stem mortality in this particular system, dead stems were almost never observed during sampling, indicating that tidal removal of dead stems is clearly still an important process.

Conclusions

Seasonal and annual density variations are interrelated. In this study, annual density measurements were taken at the end of the growing season. Seasonal measurements indicated that measurements from the end of the growing season correspond with substantially lower stem densities than measurements from the beginning of the growing season. Thus, the degree of seasonal stem loss each year was presumably influential on yearly densities, and the factors that drive seasonal loss may be partially responsible for variations in annual density as well, or may influence the relationship between environmental variables and density when it is only measured at the end of the season. Furthermore, as *S. alterniflora* is a perennial plant, densities at the end of the growing season presumably influenced the initial density of the following growing season. Initial density was shown to correspond with greater stem loss, indicating that there is a feedback loop between these annual and seasonal measurements. Thus, studying factors that influence each is important.

The well-documented variations in *S. alterniflora* density among years, within the growing season, and between systems are poorly understood. Findings such as these, which elucidate factors involved in driving variation in a particular salt marsh system, contribute to improving our knowledge of the species' ecology. Variations in *S. alterniflora* density can correspond with changes in the primary productivity of the entire salt marsh system, as well as the strength of the ecosystem services it provides to humans and the environment. Understanding plant growth responses to environmental factors is critical for calculating accurate estimates of these ecological functions, and how they are likely to change in response to current and future climatological events.

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