

When plants fight back: the role of plant chemistry in preventing herbivory-driven marsh loss

Project Description - Conceptual Framework

Saltmarsh ecosystems enhance the resilience of coastal communities by stabilizing sediments, cycling nutrients, and providing habitat for environmentally and economically important species (Barbier et al. 2011; Costanza et al. 2014). One of the greatest threats to salt marshes is accelerated sea-level rise (Morris et al. 2002; Crotty et al. 2017). Salt marshes in the mid-Atlantic of the United States experience some of the highest recorded rates of relative sea-level rise (RSLR) (Sallenger et al. 2012; Boon and Mitchell 2015), which are 3-4 times higher than the global mean (Sallenger et al. 2012). To keep up with sea-level rise, marshes must either migrate to higher ground or accrete (build up) vertically. When uninhibited by man-made barriers, marshes are able to migrate upland (Kirwan et al. 2016), however the rate and ability of the marsh to vertically accrete remains a point of concern. Marsh accretion can be controlled by physical factors such as sediment supply and hydroperiod, as well as by biotic factors such as herbivory intensity and excavations by burrowing crab species (Davidson & de Rivera 2010; Thomas & Blum 2010). Saltmarsh plants regulate marsh accretion rates by trapping sediments aboveground and contributing organic matter belowground, making plants critical to saltmarsh persistence (Morris et al. 2002; Kirwan & Megonigal 2013).

Runaway consumption by herbivores, which can remove vegetation in large areas, has been highlighted as a potential driver of marsh loss (He & Silliman 2016). However, despite the presence of herbivores, salt marshes persist. This may be due in part to how plants respond to herbivory pressure. For instance, plants in southern latitudes, where herbivory pressure is stronger, have more anti-herbivore compounds than those in the north (Long et al. 2011). This indicates that the resilience of the marsh against runaway herbivory may depend on plant response. **Thus, my overarching goal is to understand how plant chemistry can mediate the intensity and distribution of herbivory, and how this interaction can affect vertical accretion and salt marsh persistence.**

Background

Smooth cordgrass, *Spartina alterniflora* (hereafter *Spartina*) is a dominant plant in salt marshes along the Atlantic coast of the United States. Elevation plays a crucial role in the survival, growth, and reproduction of *Spartina* (Mendelssohn & Morris 2002). There are two distinct phenotypes of *Spartina*, a tall form near the marsh edge, which has lower elevation (i.e., the low marsh), and a short form at the higher elevations (i.e., the high marsh). This phenotypic plasticity is driven by a variety of biotic and abiotic factors, with elevation as one of the most important (Gallagher et al. 1988).

There are several herbivores of *Spartina*, however one herbivore of concern is the purple marsh crab, *Sesarma reticulatum* (hereafter *Sesarma*) (Bertness et al. 2014; Crotty et al. 2017). The consumption of both aboveground and belowground biomass of *Spartina* by *Sesarma* indirectly contributes to salt marsh habitat loss via a decrease in vertical accretion (Schultz et al. 2016). Although previous studies have suggested that herbivory events can lead to marsh loss (Davidson & de Rivera 2010; Bertness et al. 2014), this is not a universal response. For example, in the marshes of eastern Virginia, although there are areas of marsh edge that have been denuded of vegetation by *Sesarma*, as found in other studies (Hughes et al. 2009; Vu et al. 2017), there are also previously denuded areas where *Spartina* has revegetated, despite the presence of

Sesarma. Thus, instead of denuded marsh edge converting into mudflats as seen in other studies (Vu et al. 2017), we are seeing a narrow band of *Sesarma*-impacted areas advancing into the high marsh. **This suggests that, in some instances, salt marshes can be resilient to the effects of intense herbivory.**

In the Virginia marshes where *Sesarma* are absent, there is a gradual transition in elevation between the high and low marsh phenotypes of *Spartina*. However, in areas where *Sesarma* is present, there is a 20-30 cm scarp (Kirwan, M. unpublished data) that causes distinct zonation of the low and high marsh, with a ring of denuded marsh separating these areas (Fig.1). Although this decrease in elevation follows similar patterns set forth by models of tidal-creek elongation (Hughes et al. 2009), the low marsh did not become an unvegetated mudflat following *Sesarma* herbivory. Instead, it has been re-colonized by tall form *Spartina*, which is contrary to the expected patterns of herbivore impacts on marsh geomorphology set forth by previous studies (Hughes et al. 2009; Vu et al. 2017). This re-vegetation of the marsh edge, despite the decrease in elevation, may prevent further marsh loss through increased sediment deposition and thus vertical accretion. However, the question remains, why has *Sesarma* not eaten the *Spartina* in the revegetated areas? **I hypothesize that following grazing by *Sesarma*, alterations in the plant chemistry of recovering *Spartina* cause the tissue to become unpalatable, deterring further grazing.** This in turn allows the low marsh to revegetate and continue to accrete sediments. I will test my hypotheses in the marshes along Phillips Creek, which is part of the Virginia Coast Reserve Long-Term Ecological Research (VCR-LTER) site.

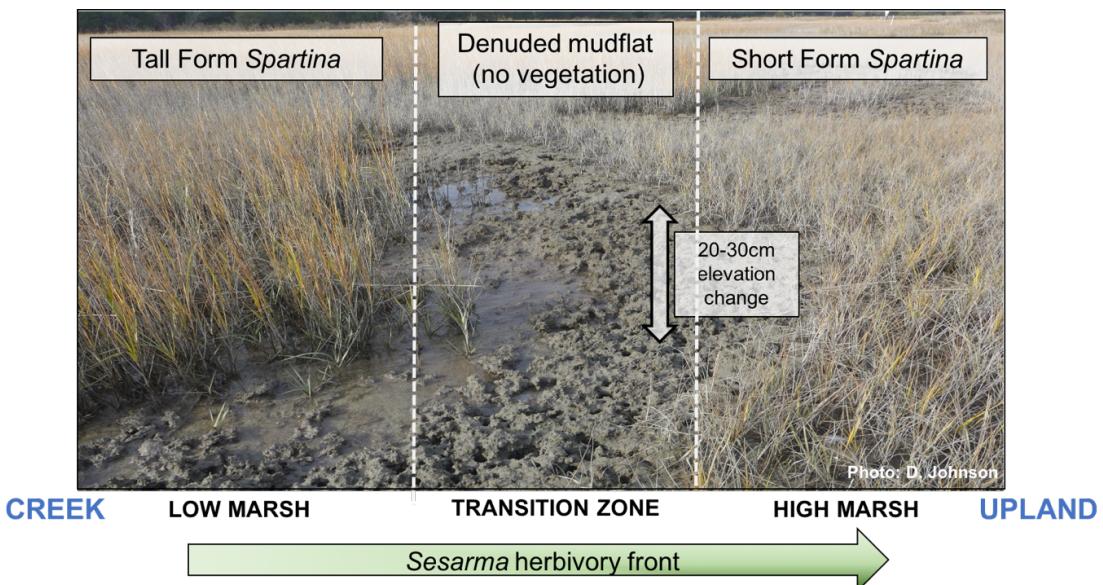


Figure 1. Phillips Creek zonation with tall and short form *Spartina* and *Sesarma* denuded area.

Objectives & Methods

Objective 1: To survey present-day conditions of the salt marsh at Phillips Creek including *Spartina* chemistry and geomorphic properties within each of the two marsh zones (tall form and short form) of *Sesarma*-impacted areas in comparison to non-impacted areas. In the summer of 2017, I collected a small subset of *Spartina* (~10 plants) from each zone of one *Sesarma*-impacted area at Phillips Creek and analyzed them for total soluble protein content. Because high protein content is a predictor of high forage quality (Cebrian et al. 2009), **I hypothesized that short form *Spartina* would have a higher protein content than the revegetated tall form,**

thus driving the position and movement of the *Sesarma* herbivory front. Preliminary results indicate that my hypothesis was correct, with tall form *Spartina* having lower levels of protein content than short form. These results follow my expectations, as the grazing front by *Sesarma* appears to be moving upland into the short form *Spartina* and away from the revegetated tall form, which may be driven by higher protein content and forage quality. However, these results are only from a small sample from one *Sesarma*-impacted area. For the summer of 2018, I will expand this survey to include more sites, greater plant replication, and more in-depth plant chemistry analyses. A greater subset (~30 plants) will be collected from each zone at four independent *Sesarma*-impacted areas within Phillips Creek and at four reference areas that are unaffected by *Sesarma*. The aboveground biomass will be analyzed for total soluble protein content as well as additional variables including: carbon and nitrogen content, total phenolic concentrations, and fiber content, as these may also contribute to the forage quality of *Spartina* (Cebrian et al. 2009). To examine accretion processes in these zones, I will measure belowground biomass (cores), soil strength (shear vane), and sediment deposition (sediment plates). In addition, I will use long-term data collected by the VCR-LTER from sediment elevation tables (SETs) near the proposed study areas to estimate the relative accretion rates in low and high marsh.

Objective 2: To determine if *Sesarma* displays preferential feeding between plants from each zone. Because forage quality can drive the distribution of herbivores, **I hypothesize that *Sesarma* prefer the higher-quality short form *Spartina* than the revegetated tall form *Spartina*.** To test this hypothesis, two feeding assays will be conducted with *Sesarma* and *Spartina*. The first assay will use fresh, live *Spartina* tissue collected from each zone, tall form and short form. *Sesarma* will be given one piece of each plant simultaneously, and the change in biomass and leaf surface area will be used to calculate consumption rates. A second assay will be run using reconstituted plant tissues in agar so that the appearance and structural complexity of each food source is identical. This assay will clarify whether *Sesarma* herbivory is deterred by chemical or structural variables (e.g. tough tissues). Each assay will be replicated ten times, using experimentally naïve crabs for each trial. I expect that the higher forage quality of short form *Spartina* will correspond with the highest consumption by *Sesarma*, and the low forage quality of tall form *Spartina* will correspond with the lowest consumption of tissue.

Objective 3: To determine the independent and interactive effects of elevation and *Sesarma* herbivory on *Spartina* plant chemistry. My first hypothesis is that the differences in plant chemistry between tall form and short form *Spartina* are driven by herbivory, meaning that when first grazed, *Spartina* alters its plant chemistry to decrease forage quality and palatability. Alternatively, these differences may be caused by elevation, which would indicate that plant chemistry is driven by environmental variables such as sediment properties or nutrient limitation. Here, I will test the effect of elevation, herbivory, and their potential combined effects on *Spartina* chemistry. I will conduct a caging and transplant experiment at three of the *Sesarma*-impacted areas, and three un-impacted areas to serve as reference sites. Using a block design (Fig. 2), *Spartina* from each of zone (tall form and short form) will be collected and reciprocally transplanted. Each transplant will be enclosed in a cage to prevent grazing (Fig 2). I will then mimic *Sesarma* herbivory via plant clipping on half of the transplants once every 2 weeks for the duration of the experiment. Approximately 3 months later, both aboveground and belowground biomass will be collected and analyzed for the same plant chemistry variables as Objective 1.

The results of this study will elucidate whether alterations in plant chemistry and geomorphology are driven by elevation, herbivory from *Sesarma*, or both factors.

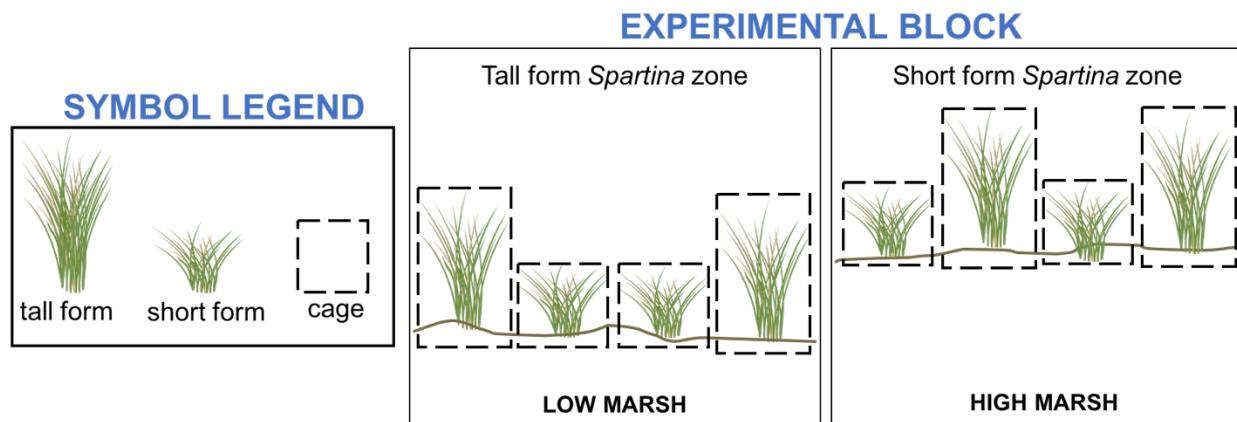


Figure 2. Representation of one experimental block for reciprocal transplant and cage installation.

Project Benefit to Coastal Wetlands

Because the Atlantic coast is experiencing one of the largest rates of relative sea-level rise in the United States, the vulnerability of these salt marshes is increasing. The ability of a salt marsh to accrete vertically is imperative to keep pace with sea-level rise, yet we still do not understand many of the underlying processes driving accretion. This research will improve our understanding of how altered plant chemistry may aid in the resiliency of salt marshes despite high herbivory pressure. The results of this research can be used in the creation and implementation of future management efforts to assist vertical accretion and thus the persistence of salt marshes under accelerating sea-level rise.

Budget

Materials & Supplies (\$2700): For the collection and processing of plant chemistry samples, I will purchase re-sealable bags, sedimentation plates, fiberglass filters, microcentrifuge tubes, pipette tips, sterile gloves, scintillation vials, tins and technician support for carbon and nitrogen processing, and a variety of chemical standards. For the feeding assays, I will purchase plastic containers to serve as experimental units, and agar to make the reconstituted *Spartina*. For the caging and transplant experiment I will purchase caging materials, excavation tools, garden pots, PVC, garden shears, re-sealable bags, zip ties, and sharpies. Travel & Lodging (\$2300): Phillips Creek is approximately 90 miles away from VIMS, and it is \$0.85 per mile to utilize a VIMS research vehicle, which totals about \$153 per roundtrip drive to the study site. I will have to make at least 10 roundtrips to this site over the course of this project, totaling \$1530. While on the eastern shore, I will be staying at the Anheuser-Busch Coastal Research Center (ABCRC) which costs \$20 per evening spent. The lodging for these multiple trips to the research site will cost approximately \$770.

Data Management & Sharing

All raw data and metadata will be formatted according to the Virginia Coast Reserve Long Term Ecological Research (VCR LTER) standards and made publicly accessible through the LTER archive. The results of this study will be presented at the Coastal Estuarine Research Federation (CERF) and the Atlantic Estuarine Research Society (AERS) meetings to increase

knowledge about coastal community resilience and salt marsh persistence in the face of sea-level rise. To inform local stakeholders of my research, I will present my results to the Nature Conservancy, who own the study site for this proposed work. I will also contribute to furthering STEM education by recruiting and mentoring an undergraduate intern for this proposed research.

Literature Cited

- Barbier, E.B. et al. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, 81(2), p. 169-193.
- Bertness, M.D. et al. (2014). Experimental predator removal causes rapid salt marsh die-off. *Ecology Letters*, 17(1), p. 830-835.
- Boon, J.D., Mitchell, M. (2015). Nonlinear change in sea level observed at North American tide stations. *Journal of Coastal Research*, 31(6), p. 1295-1305.
- Cebrian, J. et al. (2009). Producer nutritional quality controls ecosystem trophic structure. *Plos ONE*, 4(3), p. 1-5.
- Costanza, R. et al. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, 26(1), p. 152-158.
- Crotty, S.M. et al. (2017). Multiple stressors and the potential for synergistic loss of New England salt marshes. *Plos ONE*, 12(8), p. 1-13.
- Davidson, T.M., de Rivera, C. (2010). Accelerated erosion of saltmarshes infested by the non-native burrowing crustacean *Sphaeroma quoianum*. *Marine Ecology Progress Series* 419(1), p. 129-136.
- Gallagher, J.L. et al. (1988). Persistent differences in two forms of *Spartina alterniflora*: a common garden experiment. *Ecology*, 69(4), p. 1005-1008.
- He, Q., Silliman, B.R. (2016). Consumer control as a common driver of coastal vegetation worldwide. *Ecological Monographs*, 86(3), p. 278-294.
- Hughes, Z.J. et al. (2009). Rapid headward erosion of marsh creek sin response to relative sea level rise. *Geophysical Research Letters*, 36(1), p. 1-5.
- Kirwan, M. L., Megonigal, J.P. (2013). Tidal wetland stability in the face of human impacts and sea-level rise. *Nature*, 504(1), p. 53-60.
- Kirwan, M.L. et al. (2016). Sea level driven marsh expansion in a coupled model of marsh erosion and migration. *Geophysical Research Letters*, 43(1), p. 4366-4373.
- Long, J.D. et al. (2011). Local consumers induce resistance differentially between *Spartina* populations in the field. *Ecology*, 92(1), p. 180-188.
- Mendelssohn, I.A., Morris J.T. (2002). Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. In: Weinstein, M. P., Kreeger, D.A. (eds) Concepts and Controversies in Tidal Marsh Ecology. Springer, Dordrecht.
- Morris, J.T. et al. (2002). Responses of coastal wetlands to rising sea level, 83(10), p. 2869-2877.
- Sallenger Jr., A.H. et al. (2012). Hotspot of accelerated sea-level rise on the Atlantic coast of North America. *Nature Climate Change*, 2(1), p. 884-888.
- Schultz, R.A. et al. (2016). Submergence and herbivory as divergent causes of marsh loss in Long Island Sound. *Estuaries and Coasts*, 39(1), p. 1367-1375.
- Thomas, C.R., Blum, L.K. (2010). Importance of the fiddler crab *Uca pugnax* to salt marsh soil organic matter accumulation. *Marine Ecology Progress Series*, 414(1), p. 167-177.
- Vu, H.D. et al. (2017). Ecosystem engineers drive creek formation in salt marshes. *Ecology*, 98(1), p. 162-174.