Genetic Diversity and Clonal Structure of *Spartina alterniflora* in a Virginia Marsh

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Abstract

We asked how genetic diversity of *Spartina alterniflora* (smooth cordgrass) partitions across multiple spatial scales in mid-Atlantic salt marshes. Samples from five marshes, spanning ~ 35 km of coastline, were analyzed using microsatellite markers to examine genetic diversity and genotype clustering. In a single marsh, nested spatial analysis of the genotypes allowed indirect evaluation of colonization dynamics. Samples collected ≥ 10 m apart had clonal and allelic diversity levels similar to those of other geographic locations; however, genotypic richness and evenness of samples collected 0.2 and 1.0 m apart were reduced. Sampling scale had little effect on allelic diversity. Expected heterozygosity exceeded observed heterozygosity values at all sites and spatial scales, suggesting smooth cordgrass inbreeding is common in these marshes. We hypothesize that the observed spatial patterns indicate the genetic dominance of a few, well-adapted clones and is balanced by sexual reproduction and recruitment, especially after disturbance, thereby creating genetically diverse and potentially resilient marshes.

Introduction

The genetic diversity of foundational plant species are critical for structuring the broader community, enhancing species resilience, and maintaining ecosystem processes (Hughes et al. 2008, Kettenring et al. 2019, Tumas et al. 2019). For example, the genetic diversity of foundational plants, such as seagrasses, can have significant effects on primary productivity, community structure, and ecosystem functioning (Reusch and Hughes 2006, Hughes et al. 2008). *Spartina alterniflora* Loisel (smooth cordgrass) is a clonal, foundation species that is the dominant plant in salt marshes along the North American Atlantic coast from Newfoundland to Florida and the Gulf of Mexico coast (Godfrey and Wooten 1979). Along these coastlines, smooth cordgrass structures the environment by creating habitat, determining local and regional biodiversity, and controlling ecosystem dynamics (Seliskar et al. 2002, Gedan and Bertness 2010, Ellison 2019). While smooth cordgrass salt marshes provide valuable ecosystem services (Costanza et al. 1997, 2007), hydrodynamic alteration, coastal development, poor water quality and invasive species have led to widespread salt marsh decline and degradation (Gedan et al. 2009). Assessing genetic diversity of smooth cordgrass can improve our understanding of salt marsh colonization dynamics and may provide insight into how these marshes might adapt to climate change and other anthropogenic stressors.

Understanding how genetic diversity impacts the structure and function of salt marsh communities requires detailed information about how clones are spatially arranged at multiple scales – biogeographic/regional, among populations, and within populations. Studies examining the genetic diversity and spatial structure of smooth cordgrass have measured diversity across sites spanning large geographic areas (O'Brien and Freshwater 1999, Richards et al. 2004, Travis and Hester 2005, Blum et al. 2007, Novy et al. 2010, Guo et al. 2015). Most of these studies

examined population genetic diversity within the southern (south of Georgia, USA; Travis et al. 2002, Richards et al. 2004, Gaynor et al. 2019) and northern (north of New Jersey, USA; Novy et al. 2010) extent of the native range of smooth cordgrass, with few studies examining the genetic diversity of smooth cordgrass in the mid-Atlantic (but see Blum et al. 2007). Because the Virginia coast is the boundary between the Virginian and Carolinian marine biogeographic regions (Hayden et al. 1984, Ray 1988), we hypothesize that the strong latitudinal variation in climate and physical environments observed here may lead to regional differences in vegetation processes and patterns (Pennings and Bertness 1999, Pennings and Silliman 2005, Duffy 2009, Marczak et al. 2011) that could influence within-population genetic diversity (Schmidt et al. 2008).

In previous studies, sampling schemes were designed to minimize resampling the same clone(s); samples were collected ~1 m or farther apart (Utomo et al. 2009, Guo et al. 2015, Gaynor et al. 2019; Supplemental Information, Table S-1). Fine-scale spatial structure was typically ignored (but see Edwards et al. 2005, Hughes and Lotterhos 2014, Proffitt et al. 2005, Travis et al. 2004), however, the scale at which diversity is assessed is important (Vallejo-Marín et al. 2010, Binks et al. 2015). Within-site, fine spatial scales are more likely relevant to intra-species (Vallejo-Marín et al. 2010, Binks et al. 2015), plant-plant (Proffitt et al. 2005), plant-animal (Hughes et al. 2008, Noto and Hughes 2020), and plant-microbe interactions (Zogg et al. 2018, Hughes et al. 2020, Lumibao et al. 2020). Systematic measurement of genetic diversity at fine scales (i.e., $< 1\ m^2$) can provide more information on the spatial distribution of clones from which marsh plant colonization strategies can be inferred (Vallejo-Marín et al. 2010). Understanding genetic diversity at all spatial scales is important within foundational species, including salt marsh plants, because genetic diversity influences population persistence,

ecosystem function, and restoration and conservation outcomes (Seliskar et al. 2002, Booth and Grime 2003, Reusch and Hughes 2006, Hughes et al. 2008, Kettenring et al. 2014).

We present a case study from the U.S. mid-Atlantic asking how genetic diversity partitions across multiple spatial scales along the seaside of the Eastern Shore of Virginia. Using microsatellite markers, we analyzed samples from five marshes spanning ~ 35 km of coastline to compare genetic diversity levels in smooth cordgrass from Virginia to levels throughout its native range and to assess genotype clustering across the Eastern Shore of Virginia. We then measured genetic diversity and examined the spatial positions of genotypes in a single marsh at multiple scales (0.2 m, 1 m, 5 m) to indirectly evaluate smooth cordgrass colonization dynamics. Assessing genetic diversity in smooth cordgrass at multiple scales will shed light on genetic variation and colonization strategies, both of which may be critical for long-term persistence of populations (Broadhurst et al. 2008, Vallejo-Marín et al. 2010).

Methods

Field-site description

Our study sites were located along the Eastern Shore of Virginia (Fig. 1) at Upper Phillips Creek (UPC: 37° 27' 35.0244" N, 75° 50' 3.966" W), Lower Phillips Creek (LPC: 37° 27' 12.6504" N, 75° 50' 1.6512" W), Indiantown (ITM: 37° 20' 45.6972" N, 75° 54' 5.6952" W), Oyster Harbor (OHM: 37° 17' 16.7532" N, 75° 55' 45.4872" W), and Cushman's Landing (CLM: 37° 10' 29.892" N, 75° 56' 38.2164" W) salt marshes. Smooth cordgrass is the dominant plant species on the Eastern Shore (Christian and Blum 2017) as it is for most of the southeastern Atlantic coastline (Wiegert and Freeman 1990). There are two ecotypes of smooth cordgrass, a tall and a short growth form; in this study, we sampled the short-form ecotype because it is the

most common growth form on the ocean-side of the Eastern Shore. All study sites experienced similar hydrologic regimes with semi-diel tides and a tidal range of approximately 1.2 m.

Sample collection

In June 2013, we laid out a 100-m transect parallel to the tidal creek at each of the five study sites (i.e., at similar elevation and hydroperiod). At 10-m intervals along each transect, we collected a single smooth cordgrass stem, yielding a total of 50 samples to assess genetic diversity levels on the Eastern Shore. In June 2014, we used a nested approach to explore genetic diversity at multiple spatial scales (0.2 m, 1 m, 5 m) in UPC marsh (as shown in Fig. 3). At the largest scale, we sampled plant stems at 5-m intervals along a 50-m transect extending from the corner of a 10 x 10-m sampling grid. Within the 10 x 10-m sampling grid, we collected plant stems at 1-m intervals and subsampled within two randomly selected 1 x 1-m grids, where we collected plant stems at 0.2-m intervals. We collected a total of 204 samples during the 2014 sampling effort.

Genotyping

We extracted DNA from leaf tissue from the apex of each stem (3 to 5 cm in length) using QIAGEN DNeasy Mini Plant Kits (Valencia, CA) and amplified nine microsatellite loci (Blum et al. 2004; Spar01 - Spar09) using fluorescently labeled primers. We pooled ~1 µl of template DNA (consisting of 10-50 ng of total genomic DNA) in 15-µl reactions with 7.5 µl TypeIT (QIAGEN, Valencia, CA), 0.48 µl of primer mix (10µM) and 6.02 µl of molecular grade water. PCR began with a denaturing stage at 95°C (5 min) and 30 cycles of 95°C (30 s), 60°C (90 s), and 72°C (30 s), followed by a final extension stage at 60°C (30 min).

We visualized PCR products via capillary electrophoresis. Samples collected in 2013 were analyzed on a MegaBACE 1000 (GE Biosciences) with an internal ET-ROX 400 size

standard while samples collected in 2014 were analyzed on a 3730xl DNA Analyzer (Applied Biosystems) with an internal ET-ROX 500 size standard at the Georgia Genomics Facility (University of Georgia, GA). We determined fragment lengths using Fragment Profiler version 1.2 (GE Biosciences) for the 2013 samples and Geneious version 7.1 for the 2014 samples. To ensure there were no differences in fragment length due to genotyping method, we analyzed a subset of samples on both instruments for comparison and found no discrepancies.

Data analysis

We analyzed the data collected at 10-m intervals from the five study sites in 2013 separately from the data collected at three spatial scales at UPC in 2014 (UPC-0.2m, UPC-1m, UPC-5m). Several markers exhibited polyploidy (Spar02, Spar03, Spar04, Spar05 and Spar06), so we used population genetics software compatible with polyploid data. For each dataset, we assigned clonal identity to each sample in GenoDive version 3.04 (Meirmans 2020), assuming an infinite allele model with the threshold of maximum genetic distance between two individuals set to one. For each site and spatial scale, we generated the following clonal diversity measures: number of unique genotypes (num), effective number of genotypes (eff = inverse of the summed squared genotype frequencies; Legendre and Legendre 1998), evenness (evenness = eff/num; Meirmans and Van Tienderen 2004), and genotypic richness (R = num-1/n-1; Dorken et al. 2002).

For allelic diversity analyses, we removed replicate genotypes from each site to avoid allele frequency bias due to the presence of clones. We calculated observed heterozygosity, expected heterozygosity and deviation from Hardy-Weinberg equilibrium as measured by the inbreeding coefficient in GenoDive version 3.04 (Meirmans 2020) and average allelic richness per locus standardized by smallest sample size in the package ‘diveRsity’ (Keenan et al. 2013) in

142 R version 4.0.3 (R-Core-Team 2020). To investigate patterns of genotype clustering across all
143 marshes, we performed principal component analysis (PCA) on the 2013 dataset in GenoDive.
144 We plotted all samples from the 2014 dataset with their genotypic identity to visually assess
145 patterns in the spatial distribution of clones within UPC.

146 **Results**

147 The five marshes sampled in 2013 contained 37 unique genotypes out of 50 samples.
148 Each site contained a high number of genotypes relative to sample size (≥ 8 out of 10) with
149 slightly fewer effective genotypes (≥ 6.25), except for ITM (Table 1). Genotypic evenness and
150 richness were similarly high at all sites except for ITM. Across all sites and sampling schemes,
151 allelic richness ranged from 3.68 to 6.10 (Table 1). Expected heterozygosity consistently
152 exceeded observed heterozygosity, resulting in positive inbreeding coefficients, which are
153 indicative of inbreeding. The PCA revealed that genotypes did not cluster according to
154 geographic origin (Fig. 2), and the first two principal component axes accounted for a small
155 proportion of the total variance, 8.6% and 7.5%, respectively.

156 Allelic diversity patterns for all scales sampled in UPC in 2014 were similar to those
157 observed for UPC in 2013, but clonal diversity measures varied widely across scales (Table 1).
158 Across the entire area sampled in UPC in 2014, there were 67 unique genotypes and 37
159 singletons (exclusive members of a given genotype) of the 202 samples analyzed. Genotypic
160 richness at the 5-m scale was comparable to marshes sampled in 2013 (0.70) but was
161 considerably lower at the 1-m and 0.2-m scales (0.35 and 0.31, respectively). Genotypic
162 evenness was higher at the 5-m and 0.2-m scales (0.93 and 0.60, respectively) than at the 1-m
163 scale (0.34). At all spatial scales, singletons and nondominant clones were interspersed within

aggregations of dominant clones, with nearly 50 stems belonging to just two clones detected several meters apart (clones 2 and 26; Fig. 3).

Discussion

Along the seaside of the Eastern Shore of Virginia, we found clonal and allelic diversity levels similar to diversity levels reported from other geographic locations; however, spatial scale influenced some measures of genetic diversity. At the 10-m sampling scale, genotypic richness at four of the five sites exceeded 0.78 and was comparable to richness found in Gulf Coast marshes and other Atlantic marshes (Blum et al. 2007; Supplemental Information, Table S-1). However, we found that finer scale sampling (1 m and 0.2 m) reduced measures of genotypic richness and evenness. Allelic diversity remained relatively consistent at all spatial scales. Although patterns indicated that at smaller spatial scales clonal diversity decreased, we found both clustering and intermingling of genotypes at all spatial scales, with several genotypes detected within a 1-m^2 plot (Fig. 3). Additionally, expected heterozygosity values exceeded observed heterozygosity values, suggesting smooth cordgrass inbreeding is common in Eastern Shore marshes. We hypothesize that the spatial pattern of few dominant clones interspersed with several rarer genotypes and singletons could indicate that in mid-Atlantic marshes, the dominance of few, well adapted clones is balanced by sexual reproduction and recruitment. The presence of several unique genotypes and relatively high genetic diversity found for this foundation species at fine spatial scales could influence intra- and inter-species interactions, thereby impacting ecological communities and their functioning (Hughes and Lotterhos 2014, Zogg et al. 2018, Hughes et al. 2020).

Consistent with other studies examining smooth cordgrass genetic diversity at large spatial scales, genotypic richness was high at four of the five sites (> 0.78; Table 1). At these

four sites, genotypic richness was similar to Gulf Coast (0.62 – 0.95; calculated as the proportion of unique genotypes from Travis and Hester 2005), southeastern (0.88 – 1.00; calculated as genotypic richness from Gaynor et al. 2019) and mid-Atlantic and northeastern marshes (0.96 – 1.00; calculated as the proportion of unique genotypes from Blum et al. 2007). Richness and evenness were particularly low at one of our sites (ITM, 0.22) because a single clone accounted for 8 out of 10 samples along the sampling transect and extended over at least 70 m. Allelic richness at all five sites fell within the range observed for smooth cordgrass in Gulf Coast (3.09 – 4.63; Hughes and Lotterhos 2014) and southeastern (3.58 – 4.87; Gaynor et al. 2019) marshes. Our results suggest that mid-Atlantic smooth cordgrass marshes on Virginia's Eastern Shore have similar levels of genetic variation as populations throughout other parts of its native range. Although species richness is typically greater along the Eastern Shore due to the ecotone between Virginian and Carolinian marine regions, our findings do not reflect greater clonal or allelic diversity, as we had hypothesized.

The spatial scale of sampling influenced clonal diversity but not allelic diversity. Sampling at higher resolutions in UPC (at 0.2-m and 1-m intervals rather than 5-m or 10-m intervals) increased the rate of encountering stems belonging to the same genotypes, thus reducing measures of genotypic diversity and evenness (Table 1). We found both clustering (e.g., clones 1, 2, 26 and 27) and intermingling (e.g., clone 13) of dominant genotypes at all spatial scales (Fig. 3). Singletons comprised over half of the unique genotypes detected and were present at each spatial scale, indicating high rates of sexual recruitment may produce novel genotypes at UPC. In contrast, allelic diversity was robust to sampling schemes and similar across all five sites. Given that the marshes we sampled may be thousands of years old (Oertel et al. 1989a, 1989b, Brinson et al. 1995) with the exception of OHM (NOAA-NOS-NGS 2018),

similar allele frequencies across a broad area (~ 35 km) suggests there were historically few barriers to dispersal across seaside marsh populations on the Eastern Shore.

The spatial pattern of large clones interspersed with several rarer genotypes and singletons could result from vegetative expansion by dominant clones, sexual reproduction between closely related individuals, and occasional long-distance pollen or seedling dispersal. The following results support this hypothesis: we found 1) two clones with several stems distributed across the 100-m^2 sampling grid, 2) evidence of inbreeding at all sites, yet 3) no evidence of genetic differences across the five marshes. The presence of large clones indicates vegetative expansion is a successful reproductive strategy in Eastern Shore marshes, but inbreeding and genetic similarities across sites suggest sexual reproduction and rafting of clonal fragments between marshes does occur.

At all sites and spatial scales, observed heterozygosity was lower than expected heterozygosity, leading to inbreeding coefficient values ranging from 0.22 to 0.34 (Table 1). Positive inbreeding coefficients indicate this population of smooth cordgrass exhibits inbreeding and, therefore, hosts lower heterozygosity than would otherwise be expected under random mating conditions. In a range-wide survey, Blum et al. (2007) similarly found that observed heterozygosity was lower than expected for smooth cordgrass in Chesapeake Bay. Given the presence of dominant clones and evidence of inbreeding yet high genotypic diversity, we suspect seedling recruitment occurs most often from plants selfing and perhaps mating with proximal, closely related individuals. Inbreeding in marshes could result from biparental inbreeding, meaning mating between close relatives (Nuortila et al. 2006), in addition to geitonogamous selfing (Travis et al. 2004). While further analyses would be required to confirm that selfing and biparental inbreeding occur in the marshes, the highly intermingled genotypes in the UPC

provide opportunity for sexual reproduction among closely related individuals. Though we allowed a single allele mismatch within individual members of a clone to account for somatic mutations, we cannot exclude the possibility that somatic mutation – where somatic cells of clones acquire mutations as they propagate vegetatively, generating novel genotypes over time – may have contributed to the relatively high genotypic richness observed even at small spatial scales (Rogstad et al. 2002, Yu et al. 2020).

On the basis of the principal component analysis, we found little evidence of genotype clustering among smooth cordgrass from the five marshes, indicating that there is sufficient pollen or fragment dispersal across populations to prevent genetic divergence (Fig. 2). The lack of clustering within marshes studied here suggests gene flow occurs along the Eastern Shore, at least across the maximum distance between sites we sampled (~ 35 km). In northeastern marshes, smooth cordgrass genotypes from marshes spanning a much greater area encompassing New York, New Jersey, Connecticut and Rhode Island also did not cluster by site (Novy et al. 2010). Wind-driven pollen dispersal and, to a lesser extent, seed dispersal and vegetative rafting have likely contributed to the genetic similarities we observed across sites. While clonal reproduction may be a successful strategy in these marshes, occasional long-distance dispersal, at least over time scales relevant to gene flow, and inbreeding may also be important modes of reproduction in smooth cordgrass marshes.

Our cumulative findings provide support for both 'repeated seedling recruitment' (Eriksson 1989) and 'recruitment windows of opportunity' (Jelinski and Cheliak 1992) strategies for smooth cordgrass colonization, where novel genotypes are continuously created via sexual reproduction under stable conditions and sporadic disturbance enhances recruitment and establishment of novel genotypes. The intermingling of rare genotypes with dominant genotypes

256 at UPC and the genetic similarities across sites indicate recruitment may occur often.
257 Disturbances such as drought (Porter et al. 2014), salt marsh die-back (Marsh et al. 2016), deer
258 trampling (Keusenkothen 2002), and wrack deposition (Brinson et al. 1995, Tolley and Christian
259 1999) frequently occur and could provide opportunities for seeds to establish in the UPC marsh.
260 For example, in Louisiana, genetic diversity of smooth cordgrass was promoted by drought-
261 induced disturbance (Edwards et al. 2005). Additionally, in other regions, there is experimental
262 evidence that disturbance caused by burrowing crabs can stimulate sexual reproduction in marsh
263 plants (Xiao et al. 2015) and crab herbivory can increase genotypic richness in smooth cordgrass
264 (Noto and Hughes 2020). Burrowing and herbivory by crabs are common in Eastern Shore
265 marshes (Thomas and Blum 2010, Michaels and Zieman 2013) and also may contribute to the
266 high clonal diversity we observed.
267 These findings have important implications for salt marsh management along the Eastern
268 Shore because smooth cordgrass clonal and trait diversity interact to affect plant performance,
269 community interactions, and ecosystem function. For example, genotypic diversity can influence
270 plant performance metrics, such as stem density, spatial spread, and percent cover (Hughes
271 2014), and genotype identity can affect consumer activity (Zerebecki et al. 2017). Similarly,
272 plant genotype in part determines microbial community composition and diversity in smooth
273 cordgrass marshes (Zogg et al. 2018, Lumibao et al. 2020), which can indirectly affect ecosystem
274 functions, such as nutrient cycling. Bernik et al. (2018) found that heritable trait variation in
275 smooth cordgrass directly affects ecosystem function by influencing soil shear strength, which is
276 a proxy for erosion resistance (Amer et al. 2017).
277 Our findings suggest that, if other marshes exhibit similar spatial patterns of smooth
278 cordgrass genetic diversity, then managers restoring marshes and aiming to maximize diversity

may source several unique genotypes within a limited spatial extent. Further, there is minimal risk of mixing differentiated populations if source materials are collected/propagated from nearby sites because the populations are already well mixed in this region. High genetic diversity and potentially high recruitment rates in smooth cordgrass may bolster the success of marshes adapting and migrating in response to sea level rise and other stressors. A continuous supply of rarer genotypes intermingling with large, established clones can provide a form of biological insurance (Yachi and Loreau 1999), where the high number of genetically unique individuals present in a given marsh may increase the likelihood that some will be able to successfully respond to environmental change.

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Table 1. Summary genetic diversity statistics: sample size (n), number of unique genotypes (num), effective number of genotypes (eff), genotypic evenness (eve), genotypic richness (R), allelic richness (A_r), observed heterozygosity (H_o), expected heterozygosity (H_e) and inbreeding coefficient (G_{IS}). Average values are presented for results from the two grids sampled at the 0.2 m scale, with standard error of the mean included in parentheses. UPC: Upper Phillips Creek, LPC: Lower Phillips Creek, ITM: Indiantown, OHM: Oyster Harbor, CLM: Cushman's Landing.

Population	n	num	eff	eve	R	A_r	H_o	H_e	G_{IS}
2013									
UPC	10	8	6.25	0.78	0.78	4.09	0.56	0.85	0.34
LPC	10	9	8.33	0.93	0.89	3.89	0.61	0.83	0.27
ITM	10	3	1.52	0.51	0.22	3.68	0.59	0.83	0.29
OHM	10	9	8.33	0.93	0.89	4.02	0.64	0.83	0.23
CLM	10	8	7.14	0.89	0.78	4.24	0.58	0.87	0.33
2014									
UPC-5m*	11	8	6.25	0.93	0.70	4.64	0.60	0.76	0.22
UPC-1m*	121	43	14.58	0.34	0.35	6.10	0.59	0.80	0.27
UPC-0.2m	36	12 (1.4)	7.26 (0.88)	0.60 (0.002)	0.31 (0.20)	4.19 (0.01)	0.49 (0.028)	0.67 (0.001)	0.27 (0.04)

*Loci for one sample failed to amplify.

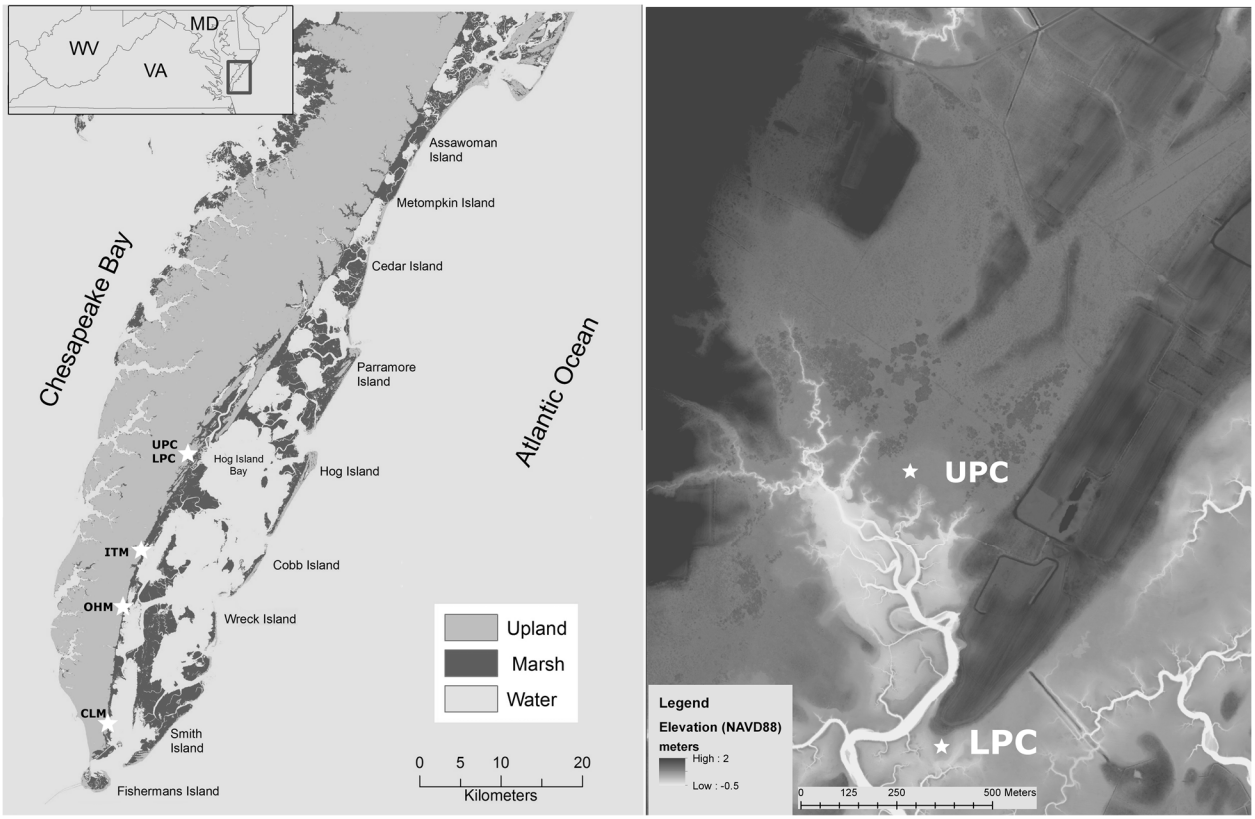


Figure 1. Sampling sites on the Eastern Shore of Virginia. Left panel: sampling locations. Right panel: LiDAR-generated elevation map of UPC and LPC marsh sites (created by J.H. Porter with data from USGS Eastern Shore, VA 2015 QL2 LiDAR, Contract: G10PC00013). UPC: Upper Phillips Creek, LPC: Lower Phillips Creek, ITM: Indiantown, OHM: Oyster Harbor, CLM: Cushman's Landing.

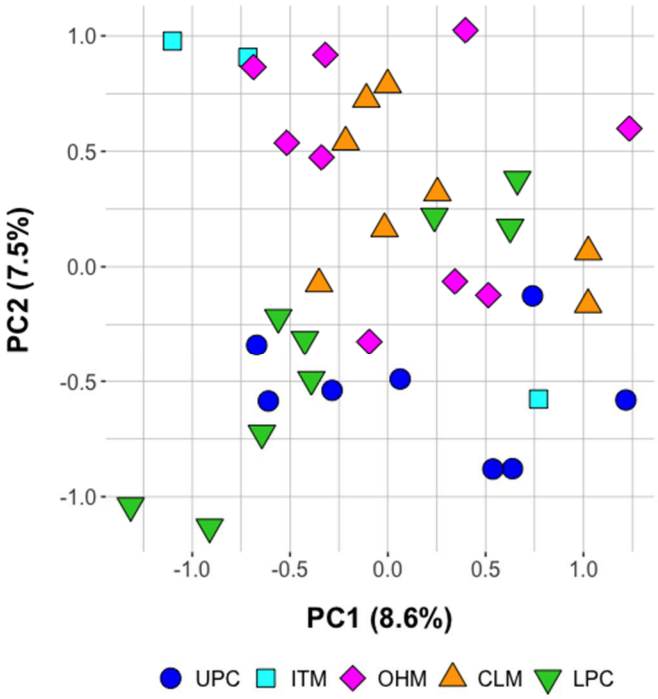
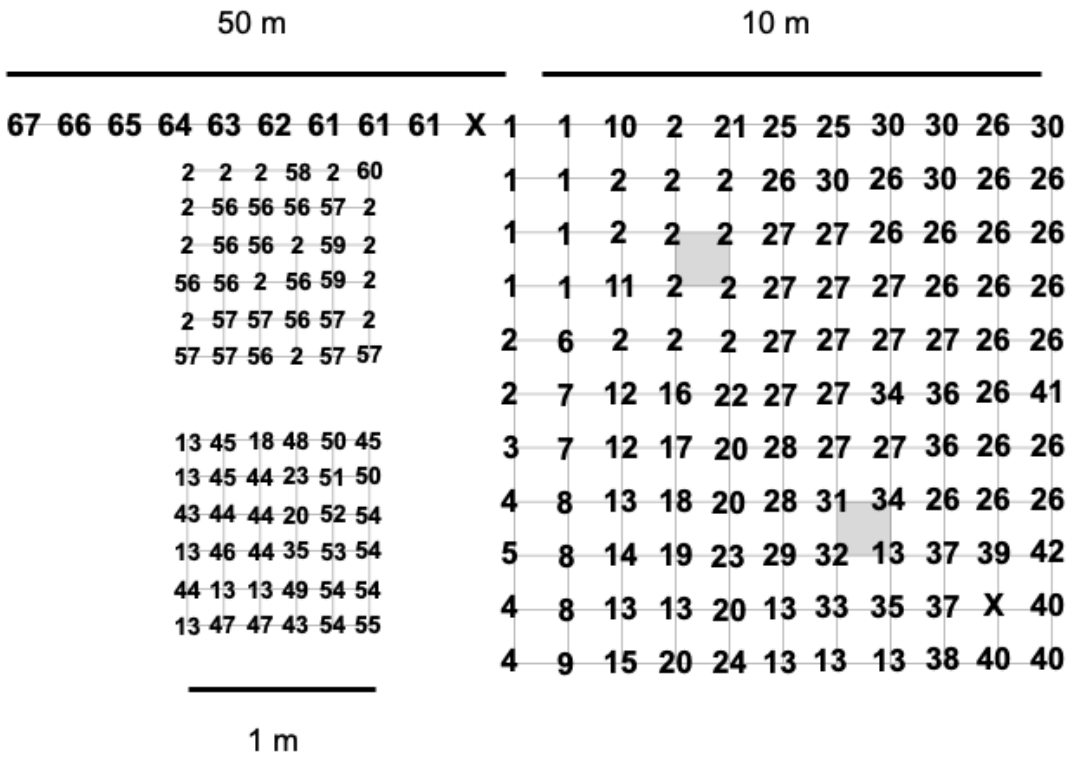


Figure 2. Principal component analysis (PCA) plot. Principal component scores are depicted for the two principal component axes explaining the greatest amount of variation, PC1 (8.6% variance) and PC2 (7.5% variance). Genotypes from each sampling location are distinguished by shape. UPC: Upper Phillips Creek, LPC: Lower Phillips Creek, ITM: Indiantown, OHM: Oyster Harbor, CLM: Cushman's Landing.



513

514 **Figure 3.** Nested spatial arrangement of the UPC genotypes (not drawn to scale). Each unique

515 genotype is numbered so that samples with shared genotypes share the same number. The 'X'

516 symbol indicates missing data (meaning loci for samples failed to amplify).

517

518

Supplemental 1

Walker, J.B., A. Bijak, and L. Blum. Genetic Diversity and Clonal Structure of *Spartina alterniflora* in a Virginia Marsh. *Northeastern Naturalist.*

Table S-1. *Spartina alterniflora* genetic papers reporting measures of genetic diversity: Clonal diversity (R or g), allelic richness (A_r), observed heterozygosity (H_o), and expected heterozygosity (H_e).

Methods: In March 2021, we used the reference data base, Web of Science/Web of Knowledge, using the key words "Spartina alterniflora" and "genetic" to search for journal articles published between 1991 and 2021 that reported measures of genetic diversity for *Spartina alterniflora*. That search yield 181 papers. We further limited the search to native range of *S. alterniflora* (North American Atlantic and Gulf Coasts). We included only papers that reported measures of population-level genetic diversity (i.e., clonal diversity, allelic richness, or observed and expected heterozygosity) and reported the spatial scale at which individual plant stems were collected. This left only the 9 papers cited in Table S-1. Not all papers included in Table S-1 used simple sequence repeats (SSR or microsatellites, the genetic markers we used) and so may not be directly comparable to our results. We included results based on other types of genetic markers (e.g., allozymes, amplified fragment length polymorphisms or AFLP, random amplified polymorphic DNA or RAPD) for the sake of completeness.

No. of plants sampled	**Clonal diversity (R)**	**Allelic richness (A_r)**	**Observed hetero-zygosity (H_o)**	**Expected hetero-zygosity (H_e)**	**Sampling distance interval (m)**	**Type of genetic markers**	**Location**
35	0.676	3.83	nr	0.551	10	SSR	Mosquito Lagoon, FL[¶¶1]
34	0.606	3.70	nr	0.543	10	SSR	Mosquito Lagoon, FL[¶1]
29	0.679	4.26	nr	0.563	10	SSR	Mosquito Lagoon, FL[¶1]
33	0.688	4.40	nr	0.608	10	SSR	Mosquito Lagoon, FL[¶1]
35	0.765	4.28	nr	0.586	10	SSR	Mosquito Lagoon, FL[¶1]
33	1	4.08	nr	0.643	10	SSR	Mosquito Lagoon, FL[1]
34	1	4.22	nr	0.568	10	SSR	Mosquito Lagoon, FL[1]
35	1	4.87	nr	0.678	10	SSR	Mosquito Lagoon, FL[1]
34	0.879	3.58	nr	0.476	10	SSR	Mosquito Lagoon, FL[1]

33		4.03	nr	0.597	10	SSR	Mosquito Lagoon, FL[¶1]
12	nr	1.79‡	0.49	0.42	10	SSR	Emerald Isle, NC[2]
12	nr	1.89‡	0.46	0.43	10	SSR	Sapelo Island, GA[2]
8	nr	1.77‡	0.63	0.42	10	SSR	Cedar Key, FL[2]
104	0.07*	3.95	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
105	0.09*	4.24	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
102	0.17*	3.63	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
103	0.14*	3.83	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
106	0.05*	3.09	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
106	0.10*	4.63	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
96	0.05*	3.80	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
102	0.07*	3.51	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
105	0.06*	3.73	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
106	0.18*	4.12	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
107	0.26*	4.60	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
103	0.23*	3.84	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
106	0.17*	3.64	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
104	0.35*	4.58	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
102	0.26*	4.41	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
135	0.08*	3.79	nr	nr	84.81 m^2§	SSR	St. Joseph Bay, FL[3]
5	nr	3.03‡	0.61	0.53	>5	SSR	Narragansett Bay, RI[4]
6	nr	5.01‡	0.73	0.65	>5	SSR	Stoningont, CT[4]
10	nr	6.63‡	0.67	0.7	>5	SSR	Jamaica Bay, NY[4]
9	nr	6.21‡	0.67	0.62	>5	SSR	Jamaica Bay, NY[4]
9	nr	3.47‡	0.72	0.75	>5	SSR	Jamaica Bay, NY[4]

5	nr	6.78‡	0.64	0.75	>5	SSR	Jamaica Bay, NY[4]
8	nr	4.71‡	0.67	0.68	>5	SSR	Mattawan, NJ[4]
3	nr	2.06‡	0.62	0.46	>5	SSR	Toms River, NJ[4]
20	0.99†	nr	0.35	0.44	2 – 5	SSR	ME[5]
8	1†	nr	0.37	0.59	2 – 5	SSR	MA[5]
14	0.99†	nr	0.51	0.51	2 – 5	SSR	MA[5]
12	1†	nr	0.34	0.5	2 – 5	SSR	MA[5]
6	0.96†	nr	0.29	0.61	2 – 5	SSR	MA[5]
11	0.99†	nr	0.3	0.54	2 – 5	SSR	MA[5]
20	0.99†	nr	0.5	0.59	2 – 5	SSR	RI[5]
3	1†	nr	0.31	0.79	2 – 5	SSR	CT[5]
19	0.99†	nr	0.44	0.59	2 – 5	SSR	CT[5]
20	0.99†	nr	0.5	0.56	2 – 5	SSR	NY[5]
20	1†	nr	0.49	0.65	2 – 5	SSR	NJ[5]
18	1†	nr	0.5	0.65	2 – 5	SSR	DE[5]
16	0.99†	nr	0.52	0.69	2 – 5	SSR	VA[5]
18	1†	nr	0.45	0.58	2 – 5	SSR	VA[5]
18	0.99†	nr	0.42	0.61	2 – 5	SSR	NC[5]
17	0.99†	nr	0.51	0.66	2 – 5	SSR	NC[5]
6	1†	nr	0.59	0.7	2 – 5	SSR	SC[5]
18	nr	62.8	0.22	nr	>200	AFLP	Barataria-Breton, LA[6]
18	nr	57.6	0.20	nr	>200	AFLP	Terrebonne, LA[6]
18	nr	55.2	0.19	nr	>200	AFLP	Mermentau, LA[6]
18	nr	60.8	0.20	nr	>200	AFLP	Calcasieu, LA[6]
170	0.82	45.46	nr	nr	0.5 – 1	AFLP	Red Pass, LA[7]
101	0.84	57.58	nr	nr	0.5 – 1	AFLP	Sabine NWR, LA[7]
129	0.95	66.67	nr	nr	0.5	AFLP	Hackberry Marsh, LA[7]
101	0.82	75.76	nr	nr	1	AFLP	Mississippi River, LA[7]
152	0.82	48.48	nr	nr	1 – 2	AFLP	Nairn, LA[7]
60	0.68	57.58	nr	nr	2	AFLP	Bay Junop, LA[7]

131	0.62	66.67	nr	nr	2.5 – 5	AFLP	Breton Sound, LA[7]
75	0.70	14.10	nr	nr	5	AFLP	Marsh Island, LA[7]
166	0.201	nr	nr	nr	0.52 – 6.28	AFLP/ RAPD	Sabine NWR, LA¶[8]
194	nr	nr	nr	nr	0.52 – 6.28	AFLP /RAPD	Sabine NWR, LA¶[8]
206	0.772	nr	nr	nr	0.52 – 6.28	AFLP/ RAPD	Sabine NWR, LA¶[8]
240	0.618	nr	nr	nr	0.52 – 6.28	AFLP/ RAPD	Sabine NWR, LA¶[8]
29	nr	31.14	0.1153	nr	< 40 ha§	AFLP	Sabine NWR, LA¶[8]
29	nr	32.02	0.1148	nr	127 ha§	AFLP	Sabine NWR, LA¶[8]
35	nr	32.02	0.1256	nr	117 ha§	AFLP	Sabine NWR, LA¶[8]
19	nr	27.63	0.1059	nr	20 ha§	AFLP	Sabine NWR, LA¶[8]
96	nr	65.4	nr	0.220	1 – 4	Allozymes	Sapelo Island, GA[9]
96	nr	65.4	nr	0.209	1 – 4	Allozymes	Sapelo Island, GA[9]
96	nr	61.5	nr	0.189	1 – 4	Allozymes	Sapelo Island, GA[9]
96	0.88	61.5	nr	0.197	1 – 4	Allozymes	Sapelo Island, GA[9]
96	0.97	61.5	nr	0.192	1 – 4	Allozymes	Sapelo Island, GA[9]

* R was not reported but calculated from sample size and number of genotypes as G-1/N-1

† clonal diversity was reported as g = G/N

‡ allelic diversity was reported as N_e (effective number of alleles)

§ area sampled was provided but inter-sample distance was not reported

¶ reported data are from restored populations

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