ECOSYSTEM CONSEQUENCES OF GENETIC VARIATION IN THE SALT MARSH ENGINEER *SPARTINA ALTERNIFLORA*

AN ABSTRACT

SUBMITTED ON THE FOURTH DAY OF DECEMBER 2015

TO THE DEPARTMENT OF

ECOLOGY & EVOLUTIONARY BIOLOGY

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

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OF

DOCTOR OF PHILOSOPHY

BY

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ABSTRACT

Ecosystem engineers can govern ecosystem dynamics, yet ecosystem consequences of trait variation within engineering species are often overlooked. Combining field and greenhouse experiments with mathematical modelling, this study aimed to assess the relative importance of heritable and non-heritable trait variation within the engineer species *Spartina alterniflora* in controlling salt marsh erosion. In the field experiment, plots along a devegetated shoreline were restored with wild and cultivated sources to test whether populations exerted different control on erosion. The greenhouse experiment investigated whether genotypic trait differences were conserved when genotypes were exposed to elevated nutrients. A modelling approach was used to extrapolate empirical findings to temporal and spatial scales involved in landform evolution, considering spatial patterns in trait variation. The field experiment revealed that erosion rates were higher in plots planted with a wild, non-local source population as compared to plots planted with cultivars or local genotypes. Differential erosion could not be explained by differences in biomass, suggesting that other traits and resource use are stronger determinants of erosion. In the greenhouse experiment, cultivars and wild genotypes exhibited trait-specific differences in phenotypic plasticity under changing nutrient availability. Nutrient regime and heritable trait differences explained 70% of observed variation in soil shear strength. Soil shear strength increased when plants received more nutrients, but plant genotype had an equal or larger influence on soil characteristics. Model simulations suggested that older marshes (with large clones) and genetically diverse marshes (with high spatial variance in soil shear strength) may experience higher mean erosion rates. However, simulations also showed that average

erosion rates are easily underestimated if the observation period is short, as variability of annual erosion rates and the probability of mass failure events were also mediated by clone size and composition. These findings illustrate that heritable and non-heritable trait variation interact with environmental conditions and landform history, together driving geomorphological processes crucial to the persistence of coastal marshes. Consideration of these interacting factors is needed when deploying ecosystem engineers for habitat restoration.

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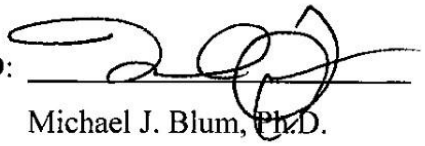

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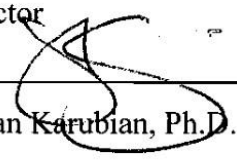

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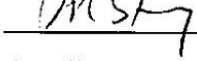

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In preparation for submission to *Journal of Applied Ecology*.

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By Brittany M. Bernik, Maarten B. Eppinga & Michael J. Blum

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CHAPTER 1. THE EXTENDED PHENOTYPE OF A LANDFORM ENGINEER: INTRASPECIFIC VARIATION AFFECTS SHORELINE EROSION IN MARSHES RESTORED USING *SPARTINA ALTERNIFLORA*

1.1 ABSTRACT

Ecosystem consequences of genetic variation are often overlooked in practical use of engineering species that modify geomorphology. Despite risks of unintended outcomes, habitat restoration projects now regularly implement agronomic approaches, including reliance on cultivars selected for specific traits to increase performance under targeted conditions. In this experiment, we considered the influence of genetic variation in the landform engineer *Spartina alterniflora* on shoreline geomorphology following restoration of a Louisiana marsh. Replicated plots on a shoreline devegetated by the Deepwater Horizon oil spill were restored using plants from one of four sources: a local natural population, a non-local natural population within the same region, and nursery stocks of two cultivated clone lines frequently used in restoration projects. We assessed variation in biomass and architectural traits directly involved in landform modification. We also measured soil strength, surface elevation, and shoreline erosion rates over a two-year period. Additionally, performance traits targeted by cultivation programs (e.g., seed production) and indicators of resource use (e.g., tissue C:N ratios and soil nutrient pools) were measured to assess whether physiological tradeoffs were correlated with ecosystem impacts of intraspecific variation. We found that cultivars did not always outperform plants from natural sources according to targeted performance traits including high

biomass production and high reproductive output. Porewater nutrient concentrations tended to be lower in cultivar plots, but no differences in soil nitrogen were observed and tissue C:N ratios suggested that low-performance plants from the non-local natural source were more strongly nitrogen limited than other plants. Erosion rates were significantly higher in the low-performance, non-local natural source plots. Accelerated erosion was not observed in the cultivar plots with comparably low biomass, suggesting that other traits and resource use are stronger determinants of erosion. This study demonstrates that intraspecific variation can result in geomorphologic consequences, and it suggests that restoration involving deployment of cultivated engineers may not yield desired outcomes, particularly under stressful condition

1.2 INTRODUCTION

Some plants that function as ecosystem engineers [1] can create and maintain habitat by modifying Earth surface processes and attributes. Referred to as geomorphologic or landform engineers (sensu [2]), these species can build and shape land by influencing the stability of surface materials and by altering material transport [3]. When an ecosystem engineer occurs at high densities over a large area, even modest amounts of genetic variation may have cascading effects on ecosystem functioning by altering the expression of functionally important traits [4]. The effects of genes at levels higher than the population, known as an *extended phenotype* (sensu [5]), are well documented [6, 7]. For example, genotypic identity in plants has been shown to affect plant and arthropod community composition, plant performance, energy flow, and nutrient cycling [6, 7]. Geomorphological components of extended phenotypes have been identified for a

number of engineering species, though the extent to which genetically based intraspecific variation influences geomorphology remains unclear [2].

Habitat restoration or creation projects employing introduced stocks of a native landform engineer present exceptional opportunities to evaluate the influence of intraspecific variation on geomorphology. Plants used in restoration projects are not only likely to be genetically different from local populations, but introduced plants also are likely to differentially express heritable functional traits shaped by local selective pressures or stochastic outcomes arising from genetic drift. Restoration projects frequently rely on plants from nurseries, which can alter local gene pools by reducing diversity, especially in projects that deploy clonal monocultures of cultivars [8, 9]. Cultivars also likely express functional traits that differ from local populations because performance traits (e.g., disease resistance, primary productivity, growth rate, and seed set) are often targeted in genetic lines under selection in nursery stocks to reduce logistical expenses, to increase establishment success, or to increase performance under stressful conditions [8, 9]. Selecting for high performance in targeted traits also can influence resource allocation to other metabolic processes, resulting in functional trade-offs [10]. For instance, selection for greater investments towards reproduction can increase costly production of flowers, fruits and seeds that in turn reduces investments in defense and growth [10].

Coastal restoration projects have extensively employed smooth cordgrass (*Spartina alterniflora*), a well-known ecosystem engineer, to vegetate and stabilize marsh shorelines against erosion, sometimes under conditions of increased inundation and tidal stress due to sea level rise [9, 11, 12]. A facultatively clonal species capable of vigorous

rhizomatous growth, *S. alterniflora* generates root mats that anchor and lend physical integrity to marsh platforms [13, 14, 15]. The presence of *S. alterniflora* root mats can prevent shoreline erosion by increasing soil shear strength by more than 500% in marsh soils, to values in excess of 4,500 Pa [14, 15]. Root density, depth, and tensile strength can all determine whether marshes are able to withstand erosive forces [13, 14, 15]. By translating to vertical shifts at the marsh surface, belowground productivity of *S. alterniflora* can also limit erosive effects by reducing tidal inundation [16]. Additionally, greater elevation can be promoted through accretion at the soil surface. Though dense aboveground canopy growth increases overall wave shear stress, it also slows water velocities and dissipates wave action, causing sediments to fall out of suspension [17, 18]. Sediments can then adhere to exposed surface area of aboveground vegetation, or can become trapped by root architecture at the soil surface, along with other particulates [18, 19]. Thus it is possible that applications of non-local *S. alterniflora* genotypes for shoreline restoration or stabilization may unintentionally contribute to marsh loss (rather than stabilization or gain) if introduced differences in functional traits reduce the dampening effect of plants on erosion rates.

It is well understood that genetic variation in *S. alterniflora* can give rise to differences in community composition and ecosystem properties. Genotypic identity can, for example, affect both recruitment and growth of co-occurring plant species via competitive suppression and facilitation [20]. Similarly, genotypic identity can determine microbial diversity within the rhizosphere [21]. Common garden transplantation experiments using *S. alterniflora* drawn from Massachusetts, Delaware, and Georgia [22] have also shown that the quantity and distribution of belowground organic matter,

edaphic algae abundance, activity of microbial communities, and presence of fish larvae can differ according to population origin [22]. Ecosystem properties bore a stronger resemblance to those at sites where plants had originated, suggesting the extended phenotype expressed by *S. alterniflora* is not sensitive to local environmental conditions [22]. Community characteristics (e.g., infaunal abundance) and ecosystem properties (e.g., light attenuation and porewater salinity) also have been found to differ among marshes in San Francisco Bay composed of native *S. foliosa*, non-native *S. alterniflora*, and invasive *S. foliosa x alterniflora* hybrids [23].

Though the extended phenotype of introduced *S. alterniflora* likely differs from that of local plants, it is not known whether use of non-local plant material in restoration projects yields favorable or intended ecosystem outcomes. Interest in the use of *S. alterniflora* cultivars has increased as a result of the 2010 Deepwater Horizon (DWH) oil spill and implementation of the 2012 Louisiana State Master Plan for coastal protection and restoration of Mississippi River delta wetlands. The DWH spill resulted in the loss of vegetation on marsh shorelines across the northern Gulf of Mexico [24, 25], and following the spill, clean-up and remediation of oiled marshes also resulted in devegetated, erosional shorelines. In this experiment, we revegetated areas of oiled and remediated marsh shoreline using different sources of natural and cultivated *S. alterniflora*. Over two years of establishment and growth, we compared plant traits, resource use, as well as soil properties and erosion rates among shoreline treatments with plants from different sources. This enabled us to test the hypothesis that post-restoration landform attributes and processes differ according to intraspecific variation. Considering the potential for tradeoffs, we also predicted that plants from natural populations would

exhibit greater capacity to reduce shoreline erosion than cultivars selected for increased reproductive performance

1.3 MATERIALS & METHODS

Source materials

We compared four source populations of *Spartina alterniflora* to examine the effect of intraspecific variation on landform engineering. We used plants from a natural population in Bay Jimmy (BJ; Plaquemines Parish, LA), the site of the experiment, to represent the landform engineering activities of locally adapted plants. Plants from a natural population in Catfish Lake (CFL; Lafourche Parish, LA)- which is a habitat similar to, but 40 km west of, Bay Jimmy- were used to capture variation in engineering activities due to trait differences among populations within a region. A nursery stock of the cultivar Vermilion (V) was used to assess outcomes related to cultivation for greater aboveground biomass production as well as tolerance to salinity and inundation [9, 26, 27]. Since 1989, salt marsh plantings along the Gulf coast have almost exclusively consisted of V. The final treatment comprised another cultivar, referred to as CP9 (CP), which enabled us to assess outcomes related to cultivation for high seed set and seed viability. The CP clone line is a derivative of crosses between V and six accessions selected for seed production that were released in 2012. These lines were developed to facilitate aerial seeding, which involves less labor and expense compared to hand-planting methods typically needed to deploy *S. alterniflora* [9, 11, 12].

Plant material was gathered so that genotypic diversity of each treatment (per unit area) approximated corresponding source populations. Thus this experiment assessed the influence of intraspecific variation among source populations that exhibit differences in

both genetic identity and genetic diversity. Microsatellite genotyping was carried out on a subset of plants used in each treatment to verify that no genotype was shared among treatments, and to characterize genetic diversity and differentiation among source treatments (detailed genetic methods and results can be found in Appendix 1). Material from BJ and CFL was gathered by harvesting plant plugs (with roots) from an area of marsh the size of an experimental plot (described below). Nurseries at Nicholls State University and the LSU AgCenter provided source material for V and CP cultivars, respectively. Though each cultivar is expected to correspond to a single genotype, additional genotypic richness among cultivar treatments is possible due to unintentional outcrossing in nursery populations (which would translate to functional contamination that might influence the outcomes of restoration projects, but does not compromise the aims of this experiment). All plant material was brought to the greenhouse, thoroughly rinsed clean, and separated into single stems for subsequent planting.

Study site and experimental design

Experimental plots were established from July to September 2011 along 400 m of shoreline in Bay Jimmy, and monitored over a period of 2 years. Bay Jimmy, which is located in northern Barataria Bay, is surrounded by salt marsh dominated by *Spartina alterniflora*. Like much of northern Barataria Bay, marshes in Bay Jimmy are highly exposed, resulting in rapid rates of peripheral erosion due to wind-driven wave stress. This exposure also allowed wave action to deliver oil to northern Barataria Bay during the 2010 Deepwater Horizon Oil Spill [24, 28]. By late June 2011, cleanup activities had largely removed contaminated vegetation and debris from Bay Jimmy, creating a ~ 10 m

devegetated shoreline zone [28]. Because the remaining underlying root mats failed to produce new emergent growth, the cleared shoreline zone provided an opportunistic location for a common garden experiment to measure the effect of intraspecific genetic variation on landform engineering, including erosion and related geomorphological attributes [25].

Using a randomized block design to control for environmental heterogeneity, the shoreline was divided into five sections (designated A–E) with replicate sets of planted plots and non-planted controls. To compare plant source treatments to unrestored shoreline, natural colonization of control plots was actively delayed until treatment plantings became fully established by cutting and removing emergent growth over the first year of the experiment. Plant source treatments and controls were each randomly assigned to one 5 m x 5 m plot per section, except for the CP treatment, which was only established in two sections due to limited availability of plant material (Fig. 1.1). Plot edges perpendicular to the shoreline were staked at 5 m and 10 m from the edge of the water, resulting in parallelogram-shaped plots for areas of curved shoreline (Fig. 1.1). Within each treatment plot, 55 bare-root stems were hand-planted approximately 45 cm apart along five rows: four rows perpendicular to shore, spaced on 90 cm centers, and the fifth row parallel to shore along the interior edge of the plots, resulting in a planting density of 2–3 stems m^{-2} (Fig. 1.2). The plots were set back 5 m from the marsh edge to allow plants time to establish prior to experiencing erosion. Plants were allowed to vegetatively expand and fill plots for a full year prior to beginning data collection, so that all measurements would reflect mature vegetation that was newly grown under common garden conditions (Fig. 1.2).

Functional and performance trait data collection

To link landform outcomes to genetically-based variation in specific traits, we quantified phenotypic differences among plants across treatments, including variation at functional and performance traits targeted by cultivation programs in order to assess whether outcomes might be related to physiological tradeoffs. In November 2013, vegetation in each treatment plot was sampled by harvesting three 10 cm diameter cores that included all aboveground (AG) and belowground (BG) tissue plus soil to a depth of 20 cm. For every plot, the area that had not eroded was divided into thirds, and a core sample was randomly collected from the interior, the middle, and the shoreward zone (Fig. 1.2). After cores were transported to the lab, AG material was harvested to measure shoot height, shoot density, inflorescence count, inflorescence length, and seed weight. Shoot measures distinguished mature shoots (i.e., with seed heads), tillers (i.e., <30 cm), and non-tillers (i.e., >30 cm). For three mature shoots per core, we recorded shoot diameter, leaf count, and leaf length (standardized by measuring the third leaf down from the seed head). BG material was divided into 10 cm intervals, roots and soil were separated, and roots were then cleaned and rinsed. Dried weights were obtained for AG and BG tissue.

Porewater and tissue nutrient data collection

To assess nutrient availability and use, nutrient pools in soil porewater were sampled in April and July 2013 using dialysis samplers (for description see [29]). A sampler was inserted into the soil at the interior boundary of each plot so that 8 wells were buried spanning 9–23 cm depth. Samplers were allowed to equilibrate for at least 3 weeks. Porewater samples were transferred from wells to 1.8 ml glass vials using a glass syringe

fitted with a nylon filter (0.45 μm pore size), completely filling vials to exclude air. Vials were immediately put into cold storage and transported to the lab for analysis. Wells that appeared contaminated (i.e., due to failure of the membrane barrier) were excluded from consideration. In April, 1.8 ml samples were taken from every well for one plot per plant source treatment, and for the remaining treatment plots, equal volumes from each well were combined into a single 1.8 ml sample. A Westco SmartChem 200 was used to spectroscopically measure concentrations of PO_4^{3-}, NH_3, and NO_x to the nearest mg L^{-1} (because NO_3^- values in preliminary trials were below detection limits, we instead analyzed NO_x, which predominantly consisted of NO_2^-). Porewater concentration values were averaged across wells for plots with samples that had not been combined prior to chemical analyses, and all porewater concentrations were log-transformed in order to attain a normal distribution.

We also examined the accumulation and allocation of nutrients taken up by plants in the different treatments by measuring tissue carbon (C) and nitrogen (N) concentrations. Dried AG and BG tissue samples from each core were ground and homogenized with a grinding mill. A CN analyzer was used to measure C and N by percent mass. For comparison, soil C and N concentrations were analyzed from dried and ground soil samples from both 10 cm intervals of the BG portion of each core.

Landform processes and attributes

To measure erosion rates within each plot, the distance between the interior edge of the plot and the shoreline was measured to the nearest cm along six transects spaced 1 m apart. Where the marsh platform was tiered, erosion measurements referred to the

uppermost platform (which vegetation was typically restricted to). Measurements were taken in September 2012, then repeated 3 months, 6 months, and 12 months thereafter. Due to the curvature of the shoreline, plots were expected to experience decreasing erosion from west to east according to the formula $P_i = P_w \cos \alpha$, where P_i is the wave power density on impact, P_w is the power density of incoming waves, and α is the angle separating the direction of wave propagation from shore-normal [30]. Thus to standardize plots, we divided erosion measures by $\cos \alpha$. Data from NOAA buoy station GISL1 was used to weight calculations by the cumulative speed of wind gusts for each direction, and satellite imagery was used to approximate α for each plot.

A soil shear vane was used to measure soil strength to the nearest k Pa in January 2014, following Turner [31]. Measurements were taken within each plot at the soil surface and at a 10 cm depth for three positions: within a clump of vegetation on the shoreline, within a clump of vegetation in the plot interior, and between clumps of vegetation in the plot interior.

To measure surface accretion and subsidence, a 1 m steel surface elevation rod was inserted into the rear section of each plot in December 2012. A face-down petri dish was threaded over each rod, pressed into the ground until it was flush against the marsh surface, and fastened firmly into place with lock nuts. Sedimentation disks (i.e., compact disks) were attached on top of petri dishes using Velcro. Accretion or erosion at each rod was measured to the nearest mm using the distance between the marsh surface and the petri dish. Measurements were taken 3 months and 9 months following installation of the rods. During measurements, accreted material was collected from each sedimentation disk and brought to the lab where it was dried to a constant mass and weighed.

Statistical Analyses

Differences in phenotypic traits among plant source treatments were tested using ANOVAs. Repeated measures ANOVAs were used to test for differences in porewater nutrient concentrations among plant source treatments over time, and ANOVAs were used to test whether tissue nutrient concentrations differed among plant source treatments. When the homogeneity of variance assumption was not met, nonparametric Kruskal-Wallis tests were used instead of ANOVAs to test for plant differences among treatment groups. All tests of significance were made at $\alpha = 0.05$, but *P* values less than 0.10 were identified as nearly significant. For all parametric tests with significant or nearly significant differences, post hoc Least Significant Difference (LSD) tests were used to determine which treatments significantly differed from another. Nonparametric post hoc comparisons were conducted using Dunn's tests.

Annual erosion rates per plot were calculated as the change in plot length, averaged across transects, between September 2012 and September 2013. An ANOVA was used to test the null hypothesis that rates of erosion did not differ among planted treatments. To compare the effect of source population with the overall effect of planting, an independent samples Mann-Whitney U test was used to test for differences in erosion between control and treatment plots due to heterogeneous variance among groups. To test the null hypothesis that surface elevation did not differ among treatments, separate ANOVAs were used for data collected in March, September, and November 2013 rather than a repeated-measured ANOVA because of differences in data availability among treatments (because some plots had eroded past the elevation pin). A factorial ANOVA was used to test the null hypothesis that soil shear strength did not differ according to

position (shoreline, interior, between plants), depth (0 cm, 10 cm), and treatment. Post hoc LSD tests were used to identify significant differences among treatments.

Though our methods (sample sizes, nested transect design, and long sampling period) are comparable to methods employed in prior studies of shoreline erosion (e.g., [32]), because the CP treatment was represented by only two plots, we assessed whether its inclusion substantively altered the results of plot-level analyses. Comparisons of analyses (i.e., with and without the CP treatment data) showed that inclusion only resulted in a slight decrease in statistical power. We thus retained the CP treatment in all analyses.

1.4 RESULTS

Genetically-based phenotypic variation among treatments

Most components of biomass varied among planted treatments in consistent ways. The V treatment exhibited significantly higher total biomass than CFL and CP, and total biomass of BJ was significantly higher than that of CP ($F_3 = 5.09$, $P = 0.004$) (Table 1.1). Significant differences in BG biomass among treatments ($F_3 = 5.59$, $P = 0.002$) followed the same pattern as total biomass (Table 1.1). Differences in BG biomass were attributable to significant variation at the 0–10 cm horizon ($F_3 = 6.23$, $P = 0.001$) rather than the 10–20 cm horizon ($K_3 = 4.80$, $P = 0.19$). Aboveground biomass was more similar among treatments ($F_3 = 2.68$, $P = 0.06$), yet all treatments exhibited significantly higher AG biomass than CP (Table 1.1). No significant differences in root to shoot (R:S) ratios were observed ($F_3 = 1.48$, $P = 0.23$; Table 1.1).

Canopy architecture varied among planted treatments in terms of height, density, shoot thickness, leaf density, and leaf length. Differences in shoot height among treatments approached significance for mature shoots ($F_3 = 2.77$, $P = 0.053$), and became significant when only tillers were excluded from comparison ($K_3 = 10.69$, $P = 0.01$). While V exhibited significantly taller mature shoots than CP and BJ, the CFL treatment exhibited significantly taller shoots than BJ overall (Table 1.2). Tiller height did not significantly differ among treatments ($K_3 = 5.31$, $P = 0.15$), indicating that height differences did not arise with the timing of shoot development. Both tiller density and total shoot density significantly differed among treatments ($F_3 = 2.91$, $P = 0.045$; $K_3 = 12.76$, $P = 0.005$), with V exhibiting densities approximately twice as high as CP (Table 1.2). The V treatment also exhibited shoot diameters that were significantly greater than both CP and CFL treatments ($F_3 = 3.92$, $P = 0.01$; Table 1.2). The number of leaves per shoot was significantly higher for BJ than for V and CFL treatments ($F_3 = 3.34$, $P = 0.02$; Table 1.2), while leaf length was significantly higher for V and BJ compared to CFL ($F_3 = 3.27$, $P = 0.03$; Table 1.2).

Unlike architectural traits, few reproductive traits varied among treatments. The average number of shoots with seed heads did not significantly differ among treatments ($K_3 = 3.37$, $P = 0.34$). While V did exhibit significantly larger seed heads than BJ ($K_3 = 9.48$, $P = 0.02$), differences were not large enough to result in differences in the total weight of seeds produced ($F_3 = 1.31$, $P = 0.28$; Table 1.2).

Nutrient variability among treatments

Porewater concentrations of some nutrients increased between April and July 2013, indicating that resources became increasingly available for uptake despite evidence of nutrient limitation among plants (Table 1.3). Temporal variation in NO_x was not statistically significant ($F_1 = 1.85$, $P = 0.20$), and there was no evidence that porewater concentrations were affected by treatment ($F_4 = 1.04$, $P = 0.43$). Significant increases in porewater NH_3 were observed over time ($F_1 = 15.46$, $P = 0.002$), and differences in NH_3 concentrations also were significant among treatments ($F_4 = 5.77$, $P = 0.01$). The CFL and control treatments showed the highest final concentrations: CFL treatments had significantly higher NH_3 concentrations than the CP treatments, and control treatments exhibited significantly higher concentrations than did the V, CP, and BJ treatments. Changes in PO_4^{3-} concentrations were variable, though an overall increase from April to July approached significance ($F_1 = 4.11$, $P = 0.07$). The BJ treatment exhibited noticeably higher PO_4^{3-} concentrations in July than did the other treatment groups, but the differences among treatments were not significant ($F_4 = 0.87$, $P = 0.51$).

Total C and N differed in tissues but not soil across the treatment groups (Table 1.1). Total C for AG biomass was significantly different among treatments ($F_3 = 3.49$, $P = 0.02$). Post hoc comparisons revealed that CP had significantly less C than CFL and BJ treatments, while C in V was intermediate between CP and other treatments (Table 1.1). Total N of AG tissue significantly differed among treatments ($F_3 = 2.89$, $P = 0.045$), with CFL having significantly lower N in AG tissue than V and BJ treatments (Table 1.1). Differences in C:N ratios for AG tissue were nearly significant, with CFL having higher ratios than V and BJ treatments, while the composition of CP was intermediate to CFL

and other treatments ($F_3 = 2.51$, $P = 0.07$; Table 1.1). Values of C and N in BG tissue did not differ among treatments ($F_3 = 1.09$, $P = 0.36$; $F_3 = 0.46$, $P = 0.71$), although CFL had noticeably lower C:N ratios than other treatments (Table 1.1). Total soil C and N did not vary among treatments ($F_3 = 0.24$, $P = 0.87$; $F_3 = 0.40$, $P = 0.75$; Table 1.1).

Landform processes and attributed among treatments

Overall, the Bay Jimmy marsh shoreline eroded an average of 1.09 m year^{-1}, at rates that decreased among experimental plots from west to east ($r^2 = 0.24$, $P = 0.02$). Without considering non-planted controls, erosion was 0.96 m year^{-1} ($r^2 = 0.33$, $p = 0.02$). Adjusting for shoreline angle reduced the west-east trend in erosion rates ($r^2 = 0.14$, $P = 0.08$) that largely reflects the gradual curve of the shoreline away from direct exposure to wind-driven waves (Fig. 1.1). The rate of angle-adjusted erosion averaged 2.03 m year^{-1} across all plots and 1.74 m year^{-1} without non-planted controls.

Adjusting for shoreline angle, plant source had a significant effect on erosion rate, explaining 35% of observed variation among the experimental plots (full model: $F_3 = 3.92$, $P = 0.03$, $r^2 = 0.35$; Fig. 1.3). Plots planted with CFL plants significantly differed from the other treatments, eroding an additional 1.88 m year^{-1} on average compared to other treatment plots (0.91 m year^{-1} unadjusted, a 128% increase). In comparison, non-planted controls eroded 1.30 m year^{-1} more on average than treatment plots (0.54 m year^{-1} unadjusted, representing a 57% increase), but eroded 1.85 m year^{-1} more than treatment plots if CFL plots were excluded from consideration. The overall difference between control and treatment plots approached significance ($F_1 = 3.13$, $P = 0.09$); the difference was significant when CFL plots were excluded from consideration ($F_1 = 8.60$, $P = 0.01$).

Differences in shear strength were significant for both depth ($F_1 = 51.59$, $P < 0.001$, partial $\eta^2 = 0.41$) and location ($F_2 = 5.86$, $P = 0.004$, partial $\eta^2 = 0.14$), with significantly higher values at the surface compared to 15 cm depths, and significantly higher values for plant clumps in the plot interior compared to either the shoreline edge or between plant clumps. While there was no evidence of an effect of plant source ($F_3 = 0.22$, $P = 0.88$), variation in soil shear strength did track differences in erosion rates among treatments (Fig. 1.3), and shear strength explained a significant amount of variation in erosion ($F_1 = 4.85$, $P = 0.04$, $r^2 = 0.24$; Fig. 1.3).

All plots experienced subsidence, but differences among treatments were not significant for any of the time periods tested (Mar. 2013: $F_3 = 0.73$, $P = 0.55$; Sep. 2013: $F_3 = 1.28$, $P = 0.35$; Nov. 2013: $F_3 = 2.27$, $P = 0.14$; Fig. 1.3). An emerging trend (Fig. 1.3) may have resulted in significant differences had monitoring continued over a longer timeframe, however, as many of the plots eroded beyond the surface elevation pins prior to the conclusion of the study, thus reducing our measurement interval.

1.5 DISCUSSION

Ecosystem consequences of intraspecific variation is often overlooked in restoration projects that rely on landform engineers to create, shape or improve habitat. To test the hypothesis that landform attributes and processes are affected by genetically-based intraspecific variation in an engineer species, we compared erosion and related properties following restoration using *Spartina alterniflora* from four source populations. We also compared variation in functional traits likely to mediate landform effects, as well as variation in performance traits and resource use that might correspond to functional trade-

offs. Our results demonstrate that the influence of intraspecific variation within *S. alterniflora* extends to landform attributes and processes, and that shoreline restoration with plants from different source populations can lead to substantially different landform outcomes. This finding subtly contrasts with evidence of variable shoreline modification by parental and hybrid *Spartina* in San Francisco Bay, which reflects occupancy of different elevations in the intertidal zone [23]. Our findings parallel prior work showing that the capacity to reduce surface erosion varies among species [33]. The importance of plant source relative to the overall ability of vegetation to buffer erosion is well illustrated in comparisons of planted treatments to non-planted controls, which show that source population had a larger effect size on erosion than planting. The observed differences in erosion among planted treatments did not reflect differences in traits expected to influence erosion (Table 1.1). Rather, variation in erosion corresponded to trait differences reflecting variation in resource uptake and allocation strategies among plants from different source populations.

Intraspecific trait variation

Evidence of genetically-based differences in traits and trait variability among cultivated, local and non-local populations corroborates prior findings of heritable phenotypic differences in *S. alterniflora* across multiple scales. For example, regional differences (i.e., among plants from sources separated by hundreds of kilometers) have been found for AG and BG biomass, root and rhizome distribution, shoot height, diameter, density, and seed head production [20, 22, 34, 35]. Comparable differences in biomass and height have been found among genotypes occurring at the same site and among sites within an

embayment [20, 22, 34]. Our findings also corroborate evidence of heritable differences in resource use. Qing *et al*. [36], for example, detected differences in N uptake and allocation (i.e., photosynthetic capacity under nutrient limitation) between *S. alterniflora* introduced to China compared to genotypes from native source populations, which suggests that functional traits and resource use may rapidly evolve in response to local selective pressures. Similarly, many of the phenotypic differences we observed among cultivars, local and non-local plants could translate to variation in individual fitness.

Though phenotypic traits and resource use differed among plants from different source populations, cultivars did not always surpass wild plants at characteristics targeted by breeding programs. For example, V cultivation has targeted AG productivity, but we found that natural populations exhibited comparable or greater AG productivity. Similarly, the CP cultivar was developed for increased fecundity, yet we found that CP plants produced the fewest seed heads and least amount of seeds per area by weight on average. Phenotypic differences among plants from different source populations extended well beyond traits targeted by cultivation, including differences that reflect trade-offs in resource allocation, such as C and N concentrations in AG tissue. This suggests that the performance of cultivars may deviate from expectation because cultivation inadvertently influences the expression of non-target traits. Thus, deploying *S. alterniflora* cultivars for shoreline restoration comes with risks of unintended organismal, population, and ecosystem outcomes.

Ecosystem and landform outcomes of intraspecific variation

The observed pattern of variation in soil shear strength suggests that intraspecific variation in belowground traits among populations can mitigate the influence of erosion on a marsh platform (Fig. 1.3). Shear strength modification is related to root abundance, or biomass per volume soil area, for *S. alterniflora* and other systems [15, 37]. Though our point measures of soil shear strength were too variable to detect a clear difference among treatments, our findings agree with prior work showing that BG interactions between plant traits and surrounding substrate can determine soil shear strength [37]. Differences in erosion among our planted treatments, however, do not appear to correspond to coarse measures of BG traits. Indeed, the treatment with the least BG biomass also experienced the least erosion (Table 1.1; Fig. 1.3). Thus, the underlying mechanism may involve more specific architectural traits of BG growth or physiological differences in resource allocation. Our findings suggest, for example, that shear strength might be driven more by root architecture than BG biomass; shear strength could be greater with lower biomass because individual roots become less impactful as root diameter increases, such that smaller roots contribute greater strength per unit area [13, 37, 38]. Evidence of lower C:N ratios in BG tissue for treatments experiencing higher erosion, compared to treatments with lower BG biomass and lower erosion, provides some support for this explanation (Table 1.2). If the relative strength of narrower roots reflects a smaller volume of area that is dominated by tissue composed of structural carbohydrates [39, 40], then lower C:N ratios could indicate the presence of thicker but less dense root networks, where overall root tensile strength and soil shear strength are comparably low.

It is also possible that the observed trends in erosion rates reflect differences in physiological responses to stress. Differences in physiological stress responses may impact soil shear strength directly, by promoting plant architectural changes like decreased root density or increased root diameter, and indirectly, by altering soil chemistry. For instance, reduced lignin content of litter or increased oxygenation can increase rates of decomposition, which decreases soil shear strength [41]. Though C:N ratios varied among the treatments, plants from all source populations exhibited relatively high ratios in AG and BG tissue, with values of N concentrations among the lowest reported in the literature [42]. This suggests that all of the plants examined in this experiment were nutrient limited. The rise in porewater ammonia observed between March and July is also suggestive of nutrient limitation and an impaired capacity to uptake resources, which can be a consequence of a number of factors in salt marsh environments including hydrocarbon contamination and salinity stress [43, 44, 45]. If so, then the distinctly lower N concentration and higher C:N ratios exhibited in AG tissue by CFL plants, which corresponded to plots with the highest erosion rate, suggest that CFL plants were more nutrient limited and possibly less capable of responding to environmental stressors than plants from the other source populations included in this study. Though CFL plants exhibited signatures of nutrient limitation (e.g., stunted AG growth), other traits (e.g., low root to shoot ratios) indicate that responses may be due to reduced nutrient transport efficiency, which would result in reduced N uptake, reduced transport of N to AG tissue, and relatively higher N concentrations in roots. Further assays of plant and soil chemistry would help resolve the nature of resource uptake and

use among *S. alterniflora* populations [46], and thereby better elucidate the controls on architectural characteristics and geochemical conditions influencing rates of erosion.

Use of cultivars for environmental restoration

While this study represents the first explicit investigation to consider how heritable intraspecific variation may influence the geomorphological fate of restored habitat, similarly minded work on foundation prairie grasses has examined whether cultivated differences in genetic composition translate to differences in ecosystem attributes following restoration. Prairie restoration, like marsh restoration, often employs cultivars, but in contrast to our findings no differences in ecosystem attributes (e.g., plant community composition, net primary productivity, C accrual, or N mineralization) have been detected in comparisons of plants from wild and cultivated seeds for a range of prairie grasses [47, 48, 49]. It is possible that the differences observed among prairies and salt marshes is a consequence of prairies harboring greater species diversity, which can reduce the relative influence of intraspecific variation in any one species on ecosystem attributes [1, 49].

Our findings suggest that genetically-based intraspecific variation can influence ecosystem integrity, and thus can dictate the success or failure of restoration efforts. Our findings also indicate that environmental factors, such as exposure to stressful conditions, can influence the expression of functional traits targeted by cultivation programs. Phenotypic plasticity, even at traits that differ among source populations, may limit performance and persistence of cultivars. Thus, accounting for the influence of intraspecific variation (including plasticity) on ecosystem processes could improve

outcomes of restoration projects and related management strategies, including provocative programs like the planned delivery of nutrient and sediment laden freshwater via massive river diversions in the lower Mississippi River Delta. It is thought that increased nutrient delivery to coastal marshes may reduce erosion by stimulating BG productivity [41], but some evidence [31] suggests that production of BG biomass is not limited by N, and that it may be reduced with the addition of phosphorus (P) in nutrient laden water. The results of this experiment indicate that genetically-based differences in resource use and allocation may shape erosion rates under different nutrient regimes. Accordingly, ecosystem models intended to characterize the outcomes of river diversions likely could be improved by circumscribing intraspecific variation in engineering species such as *S. alterniflora* at candidate locations. Models could be improved by accounting for traits besides measures of biomass production, as our findings suggest that erosion rates are more likely attributable to differences in resource allocation corresponding to variation in belowground tissue composition, root architecture, or related traits that can modify soil characteristics. Accounting for plasticity in response to the delivery of N, P, and sediment (i.e., resource uptake and allocation under favorable and stressful conditions) could further improve the likelihood of achieving intended management outcomes.

Evidence that non-local plants exhibit reduced capacity to buffer against erosion suggests that genetic variation among populations of *S. alterniflora* could give rise to eco-evolutionary feedbacks that iteratively influence the form and fate of marsh ecosystems. Work on the *Populus* system has shown that selection pressure from an external driver (i.e., beavers) can shift the genetic composition of stands and thereby alter

rates of N mineralization and decomposition which can further influence stand composition [50, 51]. Intrinsic eco-evolutionary feedbacks also have previously been implicated in the aggressive spread of *Phalaris arundinacea*, whereby genotypes that require less N produce a more recalcitrant litter layer that can tie up N supply, creating a positive feedback [4]. In contrast, our experiment uncovered intraspecific variation in modifier activities that lowered ecosystem integrity, which could result in a negative evolutionary feedback because increased land loss might select against individuals with reduced buffering capacity. Thus, genes for traits that allow increased erosion should be eliminated from the gene pool unless they possess some other fitness advantage, such as increased fecundity. Similarly, introducing cultivars targeted for improved fitness traits to a restored marsh may influence trajectories of ecosystem evolution, where alteration of the local gene pool can result in loss of function and possibly ecosystem failure due to shifts in erosion rates.

Finally, our findings suggest that the geographic distance over which intraspecific variation in *S. alterniflora* can have meaningful performance consequences may have been significantly overestimated in previous studies. It has been recommended that donor material be collected no more than 100 km from a targeted restoration site, a conservative cutoff based on results indicating that the performance of local plants was comparable to the performance of plants taken from sites more than 300 km away [34]. However, our findings indicates that genetic differences among more geographically proximate source pools can translate to meaningful trait and ecosystem variation. Indeed, plants from a source population only 40 km from the study site increased average erosion by 0.92 m $year^{-1}$. Comparisons between cultivated and natural source populations also suggests that

apparent differences in genetic variation may be contingent on prevailing environmental conditions, and therefore donor suitability may not be readily predictable according to geographic or genetic distance alone. Thus cultivation programs seeking to improve targeted traits or ecosystem attributes may need to perform in situ trials at sites slated for restoration in order to evaluate whether performance targets can be achieved under expected environmental conditions.

1.6 TABLES

Table 1.1 Measures of genetic diversity, biomass, root:shoot (R:S), C and N among four planted treatments in Bay Jimmy, LA: Vermilion (V) and CP cultivars, and Catfish Lake (CFL) and Bay Jimmy (BJ) source populations. Genetic measures include mean genotypic richness per plot (G_P) and for the whole site (G). Biomass measures include aboveground (AG), belowground (BG), and total, as well as 0–10 cm and 10–20 cm BG components. Nutrient measures are given as percent dry weight. Except genetic diversity variables, measures are averages for three cores sampled per plot, where N is the total number of cores. The number of cores used for AG and BG tissue analyses are given as N_A and N_B respectively; N_S is the number of cores used in soil analyses. Superscript letters distinguish significantly different treatments according to post hoc tests; asterisks indicate significant differences in variance; standard deviations are given in parentheses

	Genetics			Biomass (g)			BG biomass (g)			AG tissue (%)				BG tissue (%)				Soil (%)		
	N	G_P	G	AG	BG	Total	0-10	10-20	R:S	N_A	C	N	C:N	N_B	C	N	C:N	N_S	C	N
V	15	1.2	2	21.5^{A}	27.0^{A}	48.4^{A}	18.6^{A}	8.4	1.3	15	40.2^{AB}	$.5^{A}$	84.3^{A}	15	34.9	.4	109.4	15	13.2	.6
		(0.4)		(7.6)	(9.8)	(14.3)	(5.4)	(5.0)*	(0.5)		(1.2)	(.1)	(17.4)		(7.9)	(.2)	(57.8)		(5.8)	(.1)
CP	6	2.5	5	12.4^{B}	13.1^{C}	25.5^{C}	7.9^{C}	4.3*	1.2	6	39.0^{B}	$.5^{AB}$	86.9^{AB}	6	40.1	.4	124.9	6	12.8	.5
		(0.7)		(5.3)	(2.6)	(5.4)	(2.3)	(2.5)	(0.5)		(3.2)	(.1)	(33.1)		(1.9)	(.1)	(38.1)		(6.5)	(.2)
CFL	15	1.6	7	20.3^{A}	17.4^{BC}	36.3^{BC}	12.3^{BC}	5.5*	1.0	15	41.3^{A}	$.4^{B}$	104.8^{B}	10	36.8	.5	93.5	12	11.4	.5
		(0.9)		(6.4)	(6.6)	(11.0)	(5.2)	(2.7)	(0.5)		(1.3)	(.1)	(23.6)		(5.6)	(.2)	(34.9)		(5.8)	(.1)
BJ	15	1.8	6	23.1^{A}	21.8^{AB}	45.0^{AB}	15.5^{AB}	6.3	1.0	15	41.0^{A}	$.5^{A}$	86.9^{A}	14	37.7	.4	103.7	15	12.4	.6
		(0.8)		(10.2)	(7.6)	(16.0)	(6.0)	(2.7)*	(0.5)		(1.4)	(.1)	(21.9)		(6.1)	(.2)	(38.1)		(3.8)	(.1)

Table 1.2 Phenotypic traits among four planted treatments in Bay Jimmy, Louisiana: Vermilion (V) and CP cultivars, and Catfish Lake (CFL) and Bay Jimmy (BJ) source populations. Core measures are averages for all sampled cores, where the number of cores is given as *N*, mature shoots refer to those with seed heads, and total seed mass is denoted *M*. Shoot measures are averages for all sampled shoots pooled across all cores, where the number of shoots sampled is given as N_{ss}, including: stem diameter (*d*), and average lengths (*L*) of leaves and inflorescences (inflor.). Superscript letters distinguish significantly different treatments according to post hoc tests; asterisks indicate significant differences in variance; standard deviations are given in parentheses

	Core measures								**Shoot measures**				
		Shoot height (cm)			Density (.1 m^{-2})		Seed heads				Leaves		Inflor.
	N	Mature	30+ cm	< 30 cm	< 30 cm	Total	Count	*M* (g)	N_{ss}	*d* (mm)	Count	*L* (cm)	*L* (cm)
V	15	94.46^{A}	79.10^{AB}	14.41	9.53^{A}	15.33^{A}	4.27	1.68	52	5.49^{A}	7.15^{B}	31.37^{A}	17.96^{A}
		(14.09)	(11.31)*	(2.33)*	(4.16)	(4.58)*	(2.05)*	(1.41)		(1.23)	(1.97)	(8.53)	(4.83)*
CP	6	76.93^{B}	69.27^{AB}	12.47	4.50^{B}	7.83^{B}	2.67	0.53	15	4.54^{B}	7.07^{AB}	27.88^{AB}	16.78^{AB}
		(9.17)	(7.99)*	(1.86)*	(1.87)	(1.47)*	(1.37)*	(0.37)		(0.90)	(2.19)	(4.08)	(3.67)*
CFL	14	90.11^{AB}	85.21^{A}	11.50	7.36^{AB}	12.50^{AB}	4.14	1.19	46	4.72^{B}	6.82^{B}	24.94^{B}	15.83^{AB}
		(18.68)	(22.62)*	(4.14)*	(3.46)	(5.59)*	(1.66)*	(0.87)		(1.30)	(2.28)	(7.36)	(7.06)*
BJ	15	80.51^{B}	66.61^{B}	12.58	7.00^{AB}	13.20^{AB}	4.00	1.46	41	4.97^{AB}	8.22^{A}	30.54^{A}	15.40^{B}
		(17.59)	(13.80)*	(3.42)*	(3.95)	(5.29)*	(3.59)*	(1.57)		(1.44)	(2.22)	(6.98)	(6.83)*

Table 1.3 Average spring and summer 2013 porewater nutrient concentrations among four planted treatments and a non-planted control treatment established in Bay Jimmy, Louisiana. Nutrient measures include NO_x (nitrate plus nitrite), ammonia (NH_3), and phosphate (PO_4^{3-}). Concentrations are averages for all peeper wells that spanned the root zone, 9–23 cm beneath the soil surface, averaged across all plots, with corresponding sample sizes (i.e., the number of plots). Asterisks (*) indicate a significant difference between months; superscript letters distinguish significantly different treatments; standard deviations are given in parentheses

	Sample Size		NOx (mg L^{-1})		NH_3 (mg L^{-1})		PO_4^{3-} (mg L^{-1})	
Treatment	April	July	April–July		April–July*		April–July	
Vermilion	3	5	0.04 (0.02)	0.03 (0.03)	0.40 (0.21)	0.79 (0.26)^{BC}	0.35 (0.36)	1.27 (0.68)
CP	2	2	0.04 (0.01)	0.05 (0.01)	0.15 (0.20)	0.41 (0.21)^{C}	1.58 (2.11)	0.88 (0.98)
Catfish Lake	3	5	0.04 (0.02)	0.15 (0.12)	0.37 (0.20)	3.24 (4.12)^{AB}	0.77 (0.63)	2.32 (1.71)
Bay Jimmy	4	5	0.03 (0.01)	0.07 (0.07)	0.20 (0.16)	2.31 (1.43)^{BC}	1.56 (1.56)	7.56 (6.23)
Control	4	5	0.03 (0.01)	0.14 (0.17)	1.55 (0.71)	3.45 (2.17)^{A}	1.04 (0.77)	2.18 (0.44)

1.7 FIGURES

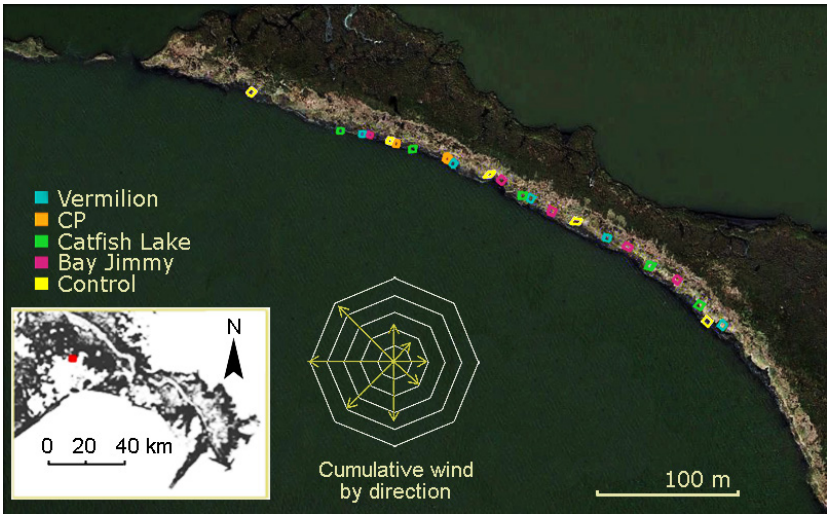

Fig. 1.1 Location of source population treatment plots in Bay Jimmy, Louisiana, and cumulative wind gust by direction from September 2012 to September 2013. The colors of outlines on the map distinguish plots planted with the Vermilion cultivar treatment, the CP cultivar treatment, the Catfish Lake source population, the Bay Jimmy source population, and non-planted control plots. Map inset depicts the site location relative to the Mississippi River outlet

Fig. 1.2 Plant source treatment plots in November 2011 and August 2012, showing how plant growth progressed from the initial plot layout and planting design. Fifty-five initial plants (pictured left) expanded to a dense meadow that often exceeded plot boundaries (pictured right)

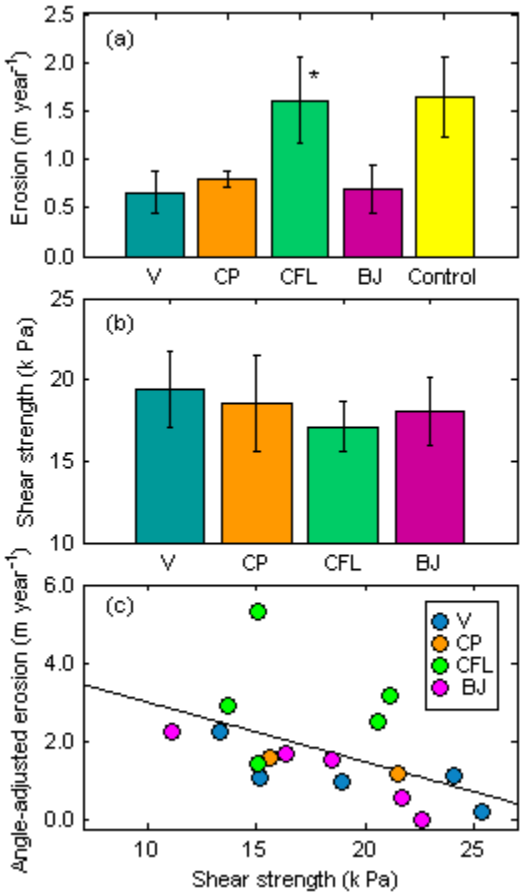

Fig. 1.3 Soil shear strength and erosion measures across planted treatments in Bay Jimmy, Louisiana. (A) Mean rates of erosion across planted treatments Vermilion (V, $N = 5$), CP ($N = 2$), Catfish Lake (CFL, $N = 5$), and Bay Jimmy (BJ, $N = 5$) and non-planted controls ($N = 5$) ($F_3 = 3.92$, $P = 0.03$). (B) Mean soil shear strength across planted treatments: V ($N = 28$), CP ($N = 10$), CFL ($N = 30$), BJ ($N = 30$) ($F_3 = 0.22$, $P = 0.88$). (C) The relationship between soil shear strength and erosion rate with different planted treatments grouped by color ($F_1 = 4.85$, $P = 0.04$, $r^2 = 0.24$)

CHAPTER 2: GENOTYPIC VARIATION IN RESPONSE OF AN ECOSYSTEM ENGINEER TO NUTRIENT AVAILABILITY

2.1 ABSTRACT

Practical applications of ecosystem engineers for habitat restoration often do not consider whether functional outcomes are contingent on heritable and non-heritable phenotypic variation. As estuarine eutrophication increases around the globe, sustaining ecosystem functions may depend on genotypic responses to nutrients. In this study, we performed a common garden greenhouse experiment to investigate how cultivated and wild genotypes of the salt marsh engineer *Spartina alterniflora* respond to changes in nutrient availability. We first examined whether phenotypic traits and nutrient uptake varied among genotypes grown under contrasting nutrient regimes. We then tested whether representative soil characteristics linked to erosion resistance paralleled plant responses to nutrient availability. We found that a spectrum of phenotypic traits and nutrient uptake differed among genotypes. Cultivars and wild genotypes also exhibited trait-specific differences in phenotypic plasticity. Nutrient regime and heritable trait differences together explained 70% of the observed variation in soil shear strength. We found that soil shear strength increased when plants received more nutrients, but that plant genotype had an equal or larger influence than nutrients on soil characteristics. These findings illustrate that heritable, non-heritable and environmental contributions can determine the fate of at-risk ecosystems like coastal marshes, which suggests that consideration should be given to all three factors when deploying ecosystem engineers for habitat restoration.

2.2 INTRODUCTION

Some engineering species can govern the integrity and fate of whole ecosystems [1, 57]. Because the direction and strength of performance of an engineer can depend on particular functional traits, ecosystem outcomes can be contingent on heritable and non-heritable phenotypic variation [4, 58]. Ecosystem-level effects constitute part of an *extended phenotype* that can vary among genotypes when trait expression has a genetic basis (*sensu* [5]). Non-heritable trait expression reflects phenotypically plastic responses to prevailing environmental conditions. Despite the ubiquity of phenotypic plasticity, the relative influence of heritable versus non-heritable trait expression on ecosystem processes is not well understood [6, 50, 59]. This is of particular concern for at-risk ecosystems dominated by clonal plants that can moderate vital ecosystem and Earth surface processes like erosion [2, 60].

Smooth cordgrass (*Spartina alterniflora*) is a salt marsh engineer that exhibits extensive variation in phenotypic traits that affect ecosystem functioning [20, 22, 34, 35]. The influence of heritable variation in *S. alterniflora* extends to the quantity and distribution of soil organic matter, microbial activity and diversity, and recruitment and growth of co-occurring plant species [20, 21, 22]. Phenotypic plasticity also likely contributes to these and other ecosystem outcomes because the expression of functional traits can be moderated by prevailing environmental conditions [36, 61]. For example, shoot height, shoot density, and belowground (BG) biomass vary according to nitrogen availability as well as stresses from sulfides, anoxia, and salinity [41, 62, 63, 64, 65, 66, 67, 68]. Prior work on genotypic variation involving reciprocal transplants indicates that ecosystem-level effects of phenotypic plasticity may be minor [22], but the full range and

importance of "extended phenotypic plasticity" may have been underestimated relative to the extended phenotype of *S. alterniflora*.

Assessing the influence of heritable variation and phenotypic plasticity on salt marsh ecosystems is timely because deployment of *S. alterniflora* cultivars is becoming a widely adopted tool for coastal management. Cultivars of *S. alterniflora* are increasingly being used to create or restore salt marsh habitat, especially in areas of the Mississippi River Delta that have experienced extensive land loss [69, 70]. For example, the cultivar known as 'Vermilion' is being used almost exclusively for restoring salt marshes along the Louisiana coast [9]. It is unclear, however, whether the extended phenotype of *S. alterniflora* cultivars differs from local genotypes, and whether use of Vermilion (or other cultivars) in restoration projects yields intended ecosystem outcomes across a range of environmental conditions. Characterizing heritable and plastic trait expression in cultivars versus local genotypes will enable more predictable outcomes of management interventions, which will help ensure delivery of valued ecosystem services, particularly as climate change continues to modify coastal environments.

The impacts of heritable and non-heritable phenotypic variation of *S. alterniflora* is central to unresolved debates about the use of river diversions and other promising management approaches for coastal marsh creation. It is unclear whether rates of erosion in the Mississippi River Delta will be ameliorated or exacerbated by river diversions that delivering nutrient laden water to marshes. Nutrient loading can, for example, reduce erosion by stimulating a net gain of BG biomass [41, 66]. Nutrient loading can also lower demand for foraging, which can allow plants to reduce BG growth as overall productivity increases [64, 65]. In addition, nutrient loading may weaken soil integrity by increasing

rates of decomposition [31]. As both productivity and soil characteristics are circumscribed by the extended phenotype of *S. alterniflora* [22, 71], the likelihood of marsh erosion may be contingent on the nature of heritable and non-heritable variation in responses to nutrient availability.

In this study, we conducted a common garden greenhouse experiment to assess heritable and non-heritable variation among *S. alterniflora* genotypes in response to nutrient loading. We compared phenotypic responses of wild and cultivated genotypes to high and low nitrate treatments, focusing on tissue chemistry traits reflecting nutrient allocation (e.g., C:N) and traits likely to influence erosion (e.g., BG productivity and architecture), as well as soil-based proxies of erosion resistance (e.g., soil shear strength). Doing so enabled us to examine: (1) whether erosion resistance differs among genotypes; (2) whether erosion resistance varies according to nutrient regime; and (3) the nature of relationships between plant traits and soil properties under different nutrient conditions. This provided a first look at the potential influence of a species' extended phenotype and extended phenotypic plasticity on ecosystem outcomes.

2.3 MATERIALS & METHODS

Wild and cultivated plant stocks

We utilized two cultivars and wild genotypes derived from two Louisiana marshes and one marsh on the northern Atlantic coast. One cultivar was 'Vermilion' (V), which was developed for aboveground biomass production, transplantation survival, and tolerance to inundation and salinity [9, 26, 27]. We also used a new cultivar line, hereafter referred to as "CP", which was developed for high seed set and germination to enable aerial seeding

for marsh creation. We obtained V and CP source material from nurseries at Nicholls State University and the LSU AgCenter, respectively. Source material for wild genotypes was collected from Bay Jimmy (BJ; Plaquemines Parish, LA) and Catfish Lake (CF; Lafourche Parish, LA), which is located approximately 40 km west of Bay Jimmy in the Barataria Basin, as well as from Jamaica Bay (New York City; NY). Donor material from all five sources was propagated in the greenhouse and grown under common garden conditions for approximately one year in order to create stocks for subsequent experiments.

Genetic characterization

Following Blum et al. [72], we assessed allelic variation across a panel of microsatellite markers to determine genotypic identity and genetic differentiation between source materials. For each source, respective individuals in an experimental group of 20 shared a single 8-locus genotype, with the exception of one individual from each of the BJ, CF, CP and NY groups. Principal components analysis (PCA) of genetic variation showed that each genotype that was unique to a single individual (i.e., *secondary* genotypes) clustered closely to the more common *primary* genotype in its respective treatment (Appendix 2.1). We also found that stocks propagated from CF plant material were genotypically indistinguishable from V, which indicates that the CF plants were either V cultivars introduced to Catfish Lake via restoration projects, or that they were admixed due to introgression of cultivar alleles into wild populations. We identified the group of individuals from the CF stock as the CF-V treatment (in reference to the apparent identity of its primary genotype but its wild source location) with the expectation that levels of

variation between CF-V and V would be minor. PCA showed that primary genotypes were broadly separated from one another, with the exception of CF-V and V genotypes (Appendix 2.1). Log-likelihood calculations assigned secondary genotypes to the correct group with 100% accuracy, and pairwise F_{ST} values indicated broad differentiation between groups (which was significant when CF-V and V were combined to allow permutation-testing; Appendix 2.2). After verifying that excluding secondary genotypes did not substantially alter results, they were retained in all subsequent analyses.

Experimental design

Starting in Apr-2013, a full factorial common garden greenhouse experiment was conducted in which genotypes were grown for approximately 6 months under control conditions and a high-nitrate nutrient treatment. For each genotype, 10 control and 10 treatment replicates were evenly divided into 5 randomized blocks. Individuals were established using whole-plant single-stems cut to 5 cm, constituting a reduction to 3-7 g starting material. To permit soil community interactions, potting material included soil collected from a salt marsh in the Point-aux-Chenes Wildlife Management Area, Louisiana, thoroughly cleaned of foreign debris and homogenized, and then mixed with sand and *Sphagnum* moss in a 2:2:3 ratio. Trade pots containing 7 L potting material were amended with 18 g Scott's Osmocote Plus (Marysville, Ohio), a patterned-release complete nutrient fertilizer containing 15% N, 9% P, and 12% K, to supply all plants an adequate base level of resources for the duration of the experiment (releasing at maximum 1.00 $g \cdot m^{-2}$ nitrate per month). Pots were placed inside buckets containing 13 L water treated with Instant Ocean® Sea Salt (Blacksburg, VA) to attain 5 ppt salinity, with

water levels approximately 3-4 cm above the soil surface after the first week of the experiment (Appendix 2.3). To minimize accumulation of salt over the soil surface, salt additions were omitted from inflows every other week, keeping concentrations to 5 ppt on average. To simulate flow-through, pots were drained of "outflow" and water was replaced with "inflow" each week, with the buckets refilled with 11 L to account for volume retained by soil saturation. For the nutrient treatment, inflow water delivered 0.69 g dissolved Hi-Yield® sodium nitrate (Bonham, TX) per pot, bringing nitrate concentrations up to 10 $mg \cdot L^{-1}$. While nitrate concentrations for the lower Mississippi River are only about 1–3 $mg \cdot L^{-1}$ on average, marshes fed by river diversions are expected to receive a median estimate of 60 $g \cdot m^{-2} \cdot y^{-1}$ nitrate due to high flow rates (with about 46% projected to be retained). We estimated that the inflow rate in our treatment delivered the equivalent of approximately 29 $g \cdot m^{-2} \cdot y^{-1}$ [73].

Phenotypic trait and soil analysis

Plant traits and soil characteristics were measured after week 28 of the experiment. Aboveground (AG) and BG growth was harvested, measured, and prepared for chemical analyses. The total number of shoots and the number of shoots with seed heads were counted for each pot. Shoot height, shoot diameter, seed head length, the number of living leaves per shoot, and live leaf lengths were measured for three mature shoots (or three shoots representing the canopy vegetation, if seed heads were not present) and averaged for each pot. The total weight of seed heads also was measured for each pot. Roots and rhizomes from upper (< 6 cm) and lower (> 6 cm) soil horizons were separated and thoroughly cleaned in cold fresh water. A hydraulic universal testing machine (MTS,

Minneapolis, MN) was then used to stretch segments of rhizome to measure the force necessary to induce failure (peak load) and to calculate ultimate tensile strength (UTS; i.e., force per area). The cross-sectional area of each rhizome segment also was recorded. Separated biomass components were then oven-dried to obtain constant mass weights for calculating ratios of AG to BG biomass (AG:BG), root to rhizome biomass (root:rhiz.), and upper to lower soil horizon biomass (BG depth ratio). For each pot, standardized dry leaf and rhizome samples were ground using a mortar and pestle. Homogenized samples were analyzed using an EA112 Element Analyzer (Thermo Scientific, Waltham, MA) to measure total carbon (C) and nitrogen (N) concentrations. Immediately after harvesting AG biomass (and prior to harvesting BG biomass), soil shear strength was measured at two points just below the soil surface (0 cm) and two points within the lower soil horizon (10 cm). Soil depth at the center and perimeter edge of each pot were measured to calculate average soil depth (prior to harvesting BG biomass).

Nutrient uptake analysis

A series of water samples were collected during week 3 and week 28 of the experiment. Using a filter-tipped glass syringe, samples were drawn through polyethylene tubing attached to each plant bucket, then transferred into glass vials and refrigerated until spectroscopic analysis (Westco SmartChem 200). During week 28, samples were taken immediately following, 48 hours after, and one week after the final inflow replacement to determine NO_2^- and NO_3^- concentrations. After week 28, the volume of outflow also was measured in order to calculate the mass abundance of retained nutrients.

Statistical analyses

Genotypic differences in nutrient removal over time were compared using repeated-measure ANOVAs. For all other variables, the effects of plant genotype and nutrient treatment were tested using factorial ANOVAs, though this offered little power to detect interaction effects (< 0.20). Due to a relationship between UTS and rhizome thickness, an ANCOVA was used to test for differences in intrinsic UTS by controlling for covariation in rhizome cross-sectional area. If transformations did not satisfy model assumptions, non-parametric Kruskal-Wallis tests were used to evaluate the effect of genotype within controls and within treatments, and to test for a nutrient effect over all samples without including genotype as a factor. The critical value was set to 0.05 for all significance tests, but post-hoc comparisons were performed when $P < 0.10$. Post-hoc comparisons evaluated the significance of pairwise differences between genotypes using LSD and Dunn's tests.

A factor analysis also was conducted to identify the major dimensions of trait variation using z-transformations of all trait variables (including outflow volume and outflow salinity, but not soil characteristics; e.g., Hester et al. 2001). Significant factors were included in a two-way MANOVA to test for differences among genotypes and nutrient treatments. Stepwise linear regression was then conducted to determine which factors explained the largest proportion of variation in each soil characteristic. Stepwise linear regression also was used to assess the effects of BG biomass and architecture, including roots versus rhizomes, on soil shear strength.

2.4 RESULTS

Trait variation among genotypes and treatments

Tissue chemistry and trait characteristics differed among genotypes; significant genotypic variation was detected for every trait examined (Figures 2.2 & 2.3), and each genotype possessed a distinct pattern of trait variation. At the end of the experiment, the number of surviving plants (N) in control and nutrient treatment for each genotype were: N_{BJ} = 2, 4; $N_{CF\text{-}V}$ = 9, 8; N_{V} = 9, 10; N_{CP} = 8, 9; and N_{NY} = 2, 8, respectively. BJ exhibited the highest mortality rates, low fecundity, and low biomass—particularly AG, despite having the longest leaves (data not shown). BJ was the only genotype to invest comparatively more in roots than in rhizomes, and had the greatest average proportion of BG biomass distributed in the shallower soil horizon (Fig. 2.1). CF-V expressed intermediate levels of most traits, including productivity and fecundity. Shoots were tall, and mean UTS was the highest of all genotypes with or without controlling for rhizome thickness. A reduced number of leaves per shoot was the only significant difference compared to V traits. The V genotype consistently expressed the highest average biomass measures, and experienced the least mortality. It produced tall shoots and the most seed heads on average, but exhibited low mean UTS values with and without controlling for rhizome thickness. The CP genotype exhibited trait tradeoffs, with the thickest shoots but the lowest shoot density, and producing large amounts of seed with few seed heads. As shoot and rhizome thickness tended to correlate (Figures 2.2 & 2.3), CP also had the thickest rhizomes on average, and the lowest UTS and highest peak load values. The NY genotype failed to produce any seed heads and exhibited the highest shoot density but the thinnest shoots and rhizomes, with the lowest average peak load values. NY also

exhibited the lowest mean UTS after controlling for rhizome thickness. NY tissue exhibited dramatically lower rhizome C:N, having 88% higher BG N concentrations on average compared to other genotypes. In addition, NY exhibited the shortest average shoot height and lowest biomass measures.

A total of eight multivariate factors explained 87.3% of the total variance across all traits (Appendix 2.4). The first factor corresponded to AG and BG biomass and explained the largest proportion of total variance (33.7%), and significantly differed among genotypes ($F_4 = 2.84$, $P = 0.03$, $\eta^2 = 0.17$). Five other factors that explained an additional 44.6% of the total variance significantly differed among genotypes: factor 2 ($F_4 = 40.93$, $P < 0.001$, $\eta^2 = 0.75$), factor 3 ($F_4 = 9.37$, $P < 0.001$, $\eta^2 = 0.41$), factor 4 ($F_4 = 5.82$, $P = 0.001$, $\eta^2 = 0.30$), factor 5 ($F_4 = 15.47$, $P < 0.001$, $\eta^2 = 0.53$); and factor 8 ($F_4 = 4.54$, $P = 0.003$; $\eta^2 = 0.25\%$; Appendix 2.4; Appendix 2.5). Based on MANOVA η^2 values, the three factors that captured the largest proportion of trait variation among genotypes were factor 2 (corresponding to C:N, shoot diameter, shoot height, shoot:root, and fecundity), factor 3 (corresponding to root:rhizome), and factor 5 (corresponding to UTS, root diameter and number of leaves; Appendix 2.4). These three factors explained 16%, 10.6%, and 7.2% of the total trait variance respectively, while genotype explained 75.2%, 40.7%, and 52.7% of the variance in each factor.

Fewer traits differed according to nutrient conditions, and shifts in nutrients typically resulted in similar or smaller effect sizes (Figures 2.2 & 2.3). Of the eight factors characterizing the majority of overall trait variation, two differed between control and elevated nutrient treatments although the proportion of variance explained by nutrients was relatively low: factor 1 ($F_1 = 9.88$, $P = 0.003$, $\eta^2 = 0.16$) and factor 2 ($F_1 =$

12.03, $P = 0.001$, $\eta^2 = 0.18$; Appendix 2.4). As described by factor 1, elevated nutrients had a positive effect on AG and BG biomass (from 0-6 cm and > 6 cm depths). As described by factor 2, shoot thickness, height, inflorescence length, and rhizome N concentration (as well as the ratio of C:N) were all significantly higher under elevated nutrient conditions (Fig. 2.1). Shoot density was also significantly higher under elevated nutrient conditions (Fig. 2.1).

Although genotypic differences in trait responses to nutrients could not be tested for statistical significance within the ANOVA framework due to relatively low power, changes in pairwise differences among genotypes using post hoc comparisons for control and elevated nutrient treatments offer some evidence of interactions (Figures 2.2 & 2.3). For traits other than shoot density, the magnitude rather than the direction of the response to elevated nutrients differed among genotypes (Figures 2.2 & 2.3). The most apparent interaction occurred with AG tissue chemistry, with leaf C:N ratios varying among genotypes and nutrient treatments. This response was also evident by a significant interaction between genotype and treatment for factor 6 ($F_4 = 5.01$, $P = 0.002$). CF-V and V genotypes also exhibited increased leaf N concentrations, while the other genotypes exhibited a decrease— particularly NY (which instead exhibited higher rhizome N concentrations). We found that while elevated nutrient conditions increased overall biomass, it had no effect on AG productivity for CP, or on BG productivity for BJ (Fig. 2.1). Additionally, while nutrients did not significantly affect the fecundity of any other genotype (including V), CF-V exhibited a 33% increase in seed heads and a 51% increase in seed mass (Fig. 2.1).

Nutrient uptake among genotypes

Nutrient outflow differed among genotypes receiving nitrate additions, with BJ and NY genotypes exhibiting lower nitrate removal efficiency (Fig. 2.3). Sample sizes for each genotype were: $N_{BJ} = 4$; $N_{CF\text{-}V} = 8$; $N_{V} = 10$; $N_{CP} = 9$; $N_{NY} = 8$; and $N_{Dead} = 11$, respectively. BJ outflow attained the highest mean NO_3^- concentration after exhibiting a large initial decline (Fig. 2.3). Genotypic differences in NO_3^- concentrations over time were not significant ($F_4 = 1.18$, $P = 0.34$). Accounting for variation in water loss, differences in NO_3^- outflow by mass were informative but not significant ($K_4 = 9.08$, $P = 0.06$). Post hoc tests indicated that mass NO_3^- outflow was significantly higher for BJ and NY genotypes than V (Dunn's test, $P < 0.05$), which is consistent with the differences observed in plant tissue N concentrations (and estimated abundance by mass). No differences were distinguished in comparison to the intermediate NO_3^- outflow of CF-V and CP. Examination of changes in NO_2^- revealed no additional N trends among genotypes ($F_4 = 0.40$, $P = 0.81$).

Soil characteristics

Soil elevation significantly increased under high nutrient conditions ($F_1 = 4.93$, $P = 0.02$, $\eta^2 = 0.08$) by 2% on average, although it did not significantly differ among genotypes ($F_4 = 0.99$, $P = 0.42$; Fig. 2.4). Changes in soil elevation were not clearly attributable to trait variation, although step-wise regression showed that factor 7 (salinity and water outflow volume) explained 7.9% of observed variation and that factor 1 (biomass) explained an additional 4.4% of observed variation ($F_2 = 5.40$, $P = 0.01$, $R^2 = 0.12$; Appendix 2.6).

Shallow soil shear strength differed among genotypes and was best explained by biomass (Fig. 4, Appendix 2.6). At the soil surface, shear strength differences among genotypes were significant within the control treatment ($K_4 = 13.73$, $P = 0.04$) and within the elevated nutrient treatment ($K_4 = 13.73$, $P = 0.01$). There was no overall nutrient effect ($K_1 = 1.14$, $P = 0.29$). Compared to the average across genotypes, soil shear strength was 43% lower for NY and 37% higher for V (but only 9% higher for CF-V). Step-wise regression indicated that factors 1, 2, 3, and 5 explain 68.4% of observed variation in soil shear strength ($F_4 = 35.10$, $P < 0.001$; Fig. 2.4). Factor 1, corresponding to biomass, explained a majority of the observed variation ($r^2 = 0.50$; Appendix 2.6). Breaking down components of BG biomass and architecture revealed that root biomass had the largest effect, explaining 66.7% of the variation at the soil surface ($P < 0.001$).

At the deeper soil horizon, shear strength significantly differed among genotypes ($F_4 = 3.92$, $P = 0.007$, $\eta^2 = 0.21$) and among nutrient treatments $F_1 = 7.17$, $P = 0.01$, $\eta^2 = 0.11$; Fig. 2.4). Over control and nutrient treatments, V exhibited 25% higher shear strength than average, while BJ and NY had 18% and 22% lower shear strength than average. Shear strength was 28% higher on average in elevated nutrient treatments. The step-wise regression model for deeper shear indicated that factors 1 and 2 explained 73.1% of the variation ($F_2 = 86.71$, $P < 0.001$), with factor 1 explaining the majority ($r^2 = 0.71$; Appendix 2.6). As found toward the surface, roots explained 60.8% of observed variation in sheer strength at depth ($P < 0.001$), whereas rhizomes explained only an additional 3.00% ($P = 0.02$).

2.5 DISCUSSION

Practical applications of ecosystem engineers for habitat restoration often do not consider whether functional outcomes are a consequence of heritable or non-heritable phenotypic variation. Using a common garden greenhouse experiment, we showed that nutrient uptake and a large set of phenotypic traits varied among genotypes of the salt marsh engineer *S. alterniflora*, including traits thought to mediate erosion resistance of soils. We also found that *S. alterniflora* genotypes exhibit phenotypic plasticity in response to elevated nutrients. The strength and direction of responses to elevated nutrients depended on genotype identity, which translated to differences in soil characteristics that are proxies of erosion resistance. While we found that erosion resistance increased when plants received more nitrate, plant genotype had an equal or larger influence on soil characteristics.

Effect traits and the extended phenotype

Genotypes differed across all functional traits measured, with phenotypic variation translating to differences in productivity and resource allocation reflected by architecture and fecundity. Thus, these traits can referred to as *effect traits*, which is defined as functional traits with ecosystem-level effects [74, 75].The effect sizes we observed are similar to what has been found in other studies, both between regional ecotypes and among local genotypes [22, 34, 61]. These findings contributed to a growing body of evidence supporting ecosystem effects of genetic variation in this and other systems, adding the first example of biogeological effects to previously observed effects on community structure [6, 21, 22, 50].

Phenotypic variation in *S. alterniflora* has in the past been interpreted as evidence of adaptation to stressor exposure resulting in morphological specialization [61, 76, 77]. However, some *S. alterniflora* genotypes function more like generalists, capable of performing well across a range of environmental conditions [61]. The V cultivar serves as an example of a generalist genotype; it exhibited comparably higher levels of performance and productivity under varying nutrient conditions, attaining high biomass and low levels of mortality, while also producing high seed set. In contrast, the CP cultivar, which has been selected for increased fecundity, produced heavier but fewer seed heads, and thus it did not exhibit specialist traits of greater overall seed production than other genotypes. Other traits distinguished the cultivars from wild genotypes, possibly due to physiological constraints or covariance. For instance, although CF-V exhibited the highest rhizome tensile strength, Vermilion exhibited rhizomes with below-average tensile strength, while CP exhibited the lowest shoot density and the thickest shoots and rhizomes. Our findings also indicate that genotypes with lower productivity may exhibit relatively constrained resource budgets due to adaptation to low nutrient conditions or reduced tolerance to stressors. For example, NY genotypes exhibited the lowest biomass and produced the fewest seeds, which may reflect the need to conserve resources under a comparatively short northern growing season.

Effect traits: nutrient responses

Though elevated nutrients resulted in greater plant biomass, fecundity, shoot diameter, height, and density, we found that genotypic differences in response to N enhancement were trait specific, which may reflect variation in resource allocation strategies. For

instance, AG biomass response was comparatively small for CP, and BG biomass response was small for BJ. Elevated nutrients had comparatively large positive effects on N concentrations in leaf tissue for CF-V and V genotypes, CF-V seed production, and NY shoot diameter and density. Phenotypic plasticity can be advantageous to plants like *S. alterniflora* that undergo vegetative reproduction, as it likely enables clonal genotypes to persist over changing environmental conditions—particularly in extreme environments like coastal salt marshes that experience salinity and inundation stress [78]. Differences between distant genotypes (e.g. NY) may reflect adaptation to broad differences in environmental conditions at different latitudes [22]. Additional work will help determine whether variation among genotypes within the same region reflects alternative response strategies to shared stressors or specialization to fine-scale spatial heterogeneities.

Our findings are consistent with prior work indicating that *S. alterniflora* exhibits intraspecific variation in nutrient uptake. Differences in sensitivity to nutrient availability have been observed among *S. alterniflora* drawn from different source populations, including differences in N uptake, allocation, and use efficiency [36]. Intraspecific variation in salt stress resistance, which can influence nutrient uptake, also has been observed among *S. alterniflora* populations [79]. Under high salinity conditions, *S. alterniflora* must invest nitrogen in glycine betaine synthesis to maintain the osmotic balance needed for water uptake and transport [80]. Individuals with a limited ability to selectively exclude or secrete salt ions also tend to invest more heavily in belowground growth [79], which is consistent with the high root:shoot ratios and rhizome N concentrations observed in the NY genotype. Variation in the ability to synthesize osmoregulatory compounds may also explain the reduced water loss and increased

nutrient outflow observed for the BJ genotype [79, 81]. Further study will be required to determine the physiological basis of genotypic variation in nutrient uptake, as the range of trait variation observed among *S. alterniflora* genotypes could reflect varying plastic responses to a combination of osmoregulation and other conditions like oxygen availability and sulfide concentration that can control nutrient uptake [82].

Though our findings indicate that plasticity differs among genotypes, suggesting that phenotypic plasticity is heritable, it is also possible that epigenetic regulation contributes to trait expression. As has been found in *S. alterniflora* and other species [78, 83, 84, 85, 86], epigenetic regulation may allow clones to respond to changing environmental conditions. This would help explain the observed differences in responses to nutrients between CF-V and Vermilion plants, which appear to exhibit the same genotype. It is possible that epigenetic regulation gradually increased the performance of clones to lower-nutrient conditions in Catfish Lake marshes, allowing clones to dynamically reduce nutrient use. Alternatively, trait expression may differ between individuals with the same genotype due to differences in genetic mutation loads accumulated over the course of clonal propagation [87]. Further assessments of rapid and cross-generational responses to shifting nutrient conditions would clarify whether epigenetic regulation contributes to marsh resilience. Doing so might also alter restoration approaches relying on predictable and consistent expression of selectively cultivated heritable traits.

Extended phenotypes: genotypic variation in erosion resistance

Soil shear strength, which serves as a proxy measure of erosion resistance, significantly varied among genotypes. Modification of soil shear strength differed among genotypes, both at the soil surface and in the rhizosphere. Evidence that the extended phenotype of *S. alterniflora* encompasses soil characteristics under common garden greenhouse conditions parallels findings from field studies where *in situ* erosion rates differed by genotype [71]. While the potential role of engineering species in modifying sediment and landform dynamics is becoming increasingly recognized, these findings are the first clear demonstration that intraspecific genetic variation contributes to biogeomorphic processes [2].

After accounting for overall plant productivity measures, the factors that best explained variation in shear strength corresponded to the traits that distinguished different genotypes. This is consistent with evidence from a field experiment [71] indicating that genotypic differences in erosion rates are likely due to finer measures of trait variation than variation in BG biomass or shear strength. Here, we found evidence of a more subtle mechanism of soil modification, whereby the magnitude of the positive effect of BG biomass on shear strength is mediated by the relative allocation to fine root production versus rhizomes, with greater fine root production accounting for a higher proportion of the variation in shear strength.

Soil shear strength measures may not fully capture the effect of root tensile strength (i.e., UTS) on the erosion resistance of the roots and rhizomes interconnected in a networked rhizome-root mat. The overall shear strength for a portion of a root mat is likely to vary as the product of UTS and the total cross sectional area of roots and

rhizomes that must break for shearing to occur [13, 14, 15]. Here, we confirmed that *S. alterniflora* exhibits the inverse power relationship between root diameter and tensile strength that has been observed in other systems [13, 37, 88] (Supplementary Fig. 3.5). We also found, however, that both attributes varied among genotypes, and that characteristics of BG biomass do not necessarily provide optimal reinforcement of the marsh platform. For example, the CP genotype had thick rhizomes that could withstand the highest force (e.g., peak load), and exhibited the lowest UTS. However, the genotype from NY exhibited the thinnest rhizomes but did not exceed the UTS exhibited by other genotypes, indicating that NY rhizomes are intrinsically weaker compared to other genotypes (Fig. 2.2). Low UTS and intrinsically weaker rhizomes were also observed for the Vermilion cultivar, in contrast to the high UTS values of CF-V (Fig. 2.2).

It remains possible, of course, that traits expressed by cultivars influence erosion resistance by modifying soil characteristics- other than elevation and shear strength- that are better characterized in field-scale experiments. AG characteristics including shoot diameter and density, for example, have been shown to promote accretion under field conditions [16, 89] by trapping particles or allowing particles to settle as a consequence of reduced water velocity [17, 18, 19, 90, 91, 92, 93]. Plant biomass turnover also contributes to accumulated organic matter, and genotypic differences in leaf litter quality could affect rates of decomposition [94].

Extended phenotype plasticity: responses to nutrient enhancement

Nutrient addition resulted in increased surface elevation and it led to responses that increased measures of erosion resistance among all genotypes. A positive effect of

nutrients on surface elevation was driven by greater plasticity, particularly in BJ and CF-V genotypes, dampening differences in heritable variation among genotypes. One of the few previous experiments examining extended phenotypes across environmental gradients found a similar effect among *Phalaris arundinacea* genotypes, in which trait differences only occurred under nutrient conditions that conferred a competitive advantage to specialists [58]. The extended phenotype of *S. alterniflora* also expressed variation that was conserved across nutrient regimes. Deep soil shear strength was similarly plastic among most genotypes, but nutrient enhancement induced larger absolute responses for genotypes exhibiting higher soil shear strength.

Extended phenotype plasticity was smaller relative to the range of heritable phenotypic differences among *S. alterniflora* genotypes. This is in agreement with previous transplantation experiments [22]. Notably, this finding provides an intriguing counterexample to a well-documented and often-cited extended phenotype, *Populus tremuloides* [50]. Effects of *P. tremuloides* genotypes on leaf litter decomposition and nutrient cycling are also moderated by nutrient regime, where effects of nutrients are larger than genotypic effects [95]. By contrast, we observed that the effect of *S. alterniflora* genotype on erosion resistance equaled or exceeded the effect of nutrients. Genotypic variation explained twice as much of observed variation in soil shear strength at depth and significantly influenced surface shear strength. It is possible, however, that the effect of nutrients may have been reduced by genotypic variation in nutrient uptake, genotypic variation in plant growth characteristics, or differences in the effects of nutrients on biomass. To understand the effect nutrient loading will have on marsh

biogeomorphology, it is therefore important to consider plant responses at the genotype level.

Management implications

Understanding responses of *S. alterniflora* to increased nutrient delivery is central to determining whether river diversions will increase or decrease rates of salt marsh erosion [31, 41]. We found that elevated nutrients resulted in greater biomass, fecundity, as well as shifts in architecture, but that trait specific responses to N enhancement varied among genotypes, possibly reflecting variation in resource allocation strategies. Additionally, we found that nutrient addition resulted in increased surface elevation and lower erosion resistance. These findings are in agreement with Morris et al. [41], who suggest that nitrate availability will not reduce net BG contributions to soil strength despite possible reduction in BG biomass relative to AG biomass [64, 65]. We did not find evidence that nitrate decreased root:shoot ratios for any of the studied genotypes. Genotypic variation also explained twice as much of observed variation in soil shear strength at depth, and genotypic differences in response to nutrient enhancement were trait specific, likely reflecting variation in resource allocation strategies. Further, we found that finer-scale characteristics of plant growth, such as root:rhizome ratio and rhizome tensile strength, may also govern erosion resistance, and that these traits differed among genotypes. These findings suggest that ecosystem outcomes of coastal restoration projects such as river diversions may be contingent on the genetic composition of resident ecosystem engineers as much as, or more so, than prevailing environmental conditions. Notably, we found no evidence that cultivation of *S. alterniflora* for targeted traits has resulted in functional

trade-offs that diminish erosion resistance. However, in light of the wide genotypic variation in effect traits and evidence of effect trait plasticity, restoration programs should evaluate whether cultivars achieve performance targets at sites targeted for use.

2.6 FIGURES

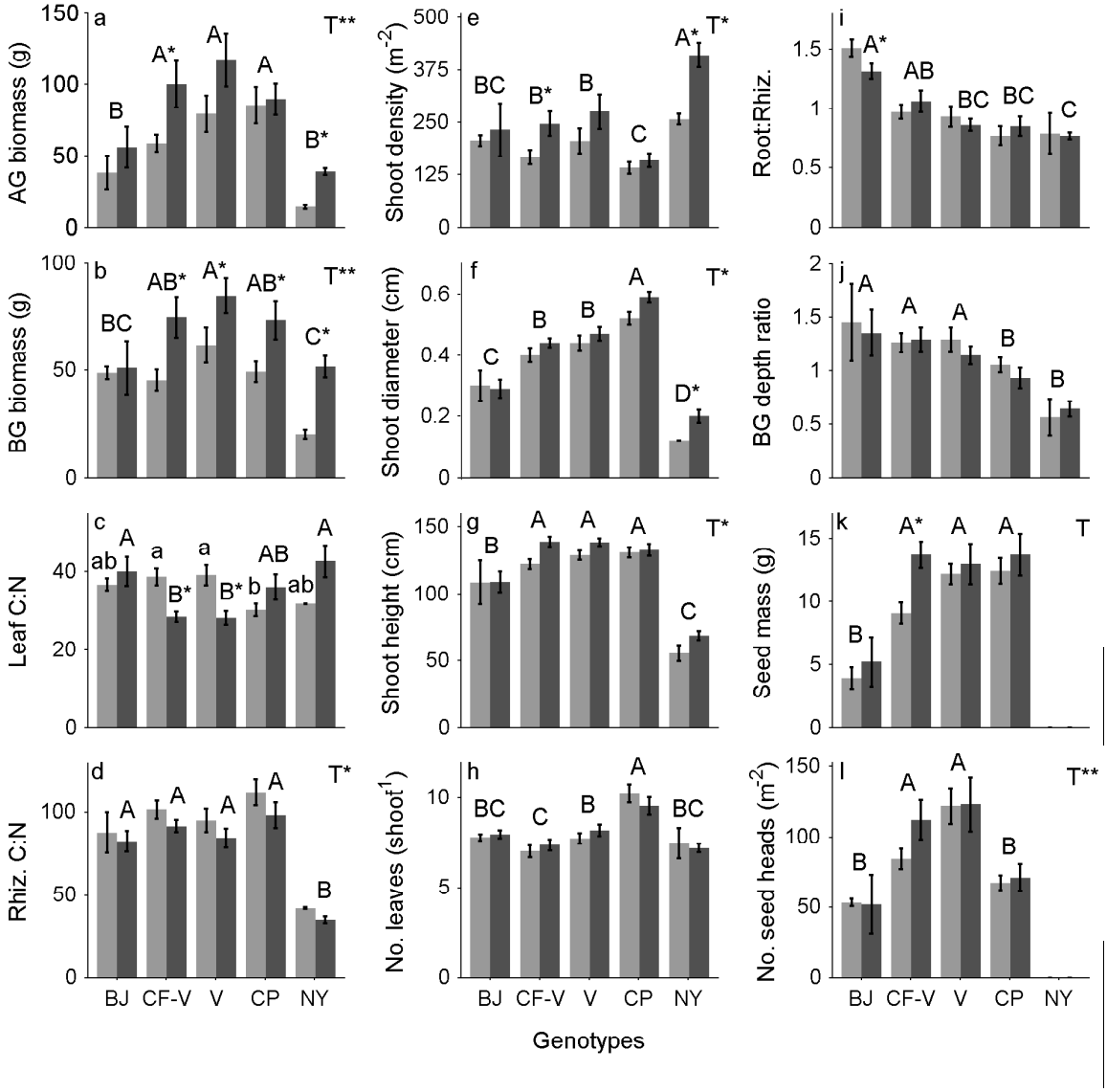

Fig. 2.1 Trait differences (mean ± SE) among Bay Jimmy (BJ), Catfish Lake (CF-V), Vermilion (V), CP, and New York (NY) genotypes of *Spartina alterniflora* after 28 weeks of growth under control and elevated nitrate treatments; for (a) *aboveground* (AG) *biomass* (genotype effect: $F_4 = 12.21$, $P < 0.001$, $\eta^2 = 0.45$; nutrient effect: $F_1 = 11.85$, $P = 0.001$, $\eta^2 = 0.17$); (b) *belowground* (BG) *biomass* (genotype effect: $F_4 = 4.53$, $P = 0.003$, $\eta^2 = 0.24$; nutrient effect: $F_1 = 13.45$, $P = 0.001$, $\eta^2 = 0.19$; (c) *leaf C:N ratio*

(genotype effect within controls: $K_4 = 11.50$, $P = 0.02$; genotype effect within the elevated nutrient treatment: $K_4 = 15.47$, $P = 0.004$; nutrient effect: $K_1 = 1.68$, $P = 0.2$); (d) *rhizome C:N ratio* (genotype effect within controls: $K_4 = 8.65$, $P = 0.07$; genotype effect within the elevated nutrient treatment: $K_4 = 21.48$, $P < 0.001$; nutrient effect: $K_1 = 6.06$, $P = 0.01$); (e) *shoot density* (genotype effect: $F_4 = 6.30$, $P < 0.001$, $\eta^2 = 0.30$; nutrient effect: $F_1 = 6.79$, $P = 0.01$, $\eta^2 = 0.10$); (f) *shoot diameter* (genotype effect: $F_4 = 56.97$, $P < 0.001$, $\eta^2 = 0.79$; nutrient effect: $F_1 = 6.09$, $P = 0.02$, $\eta^2 = 0.09$); (g) *shoot height* (genotype effect $F_4 = 56.40$, $P < 0.001$, $\eta^2 = 0.79$; nutrient effect: $F_1 = 6.79$, $P = 0.01$, $\eta^2 = 0.10$); (h) *number of leaves* (genotype effect: $F_4 = 16.38$, $P < 0.001$, $\eta^2 = 0.53$; nutrient effect ($F_1 = 0.00$, $P = 0.99$); (i) *root:rhizome ratio* (genotype effect within controls: $K_4 = 8.64$, $P = 0.07$; genotype effect within the elevated nutrient treatment: $K_4 = 14.48$, $P = 0.01$; nutrient effect: $K_1 = 1.59$, $P = 0.21$); (j) *BG depth ratio* (genotype effect: $F_4 = 11.28$, $P < 0.001$, $\eta^2 = 0.44$; nutrient effect: $F_1 = 0.38$, $P = 0.54$); (k) *seed mass* (genotype effect: $F_3 = 7.92$, $P < 0.001$, $\eta^2 = 0.32$; nutrient effect: $F_1 = 3.29$, $P = 0.08$, $\eta^2 = 0.06$); (l) *number of seed heads* (genotype effect: $F_3 = 7.21$, $P < 0.001$, $\eta^2 = 0.30$; nutrient effect: $F_1 = 0.62$, $P = 0.43$). At the top right of each panel, T indicates nutrient effect $P < 1.0$, T* $P < 0.05$, T** $P < 0.01$. Above bars, * indicates genotypes with a significant nutrient effect, letters indicate significant pairwise differences among genotypes

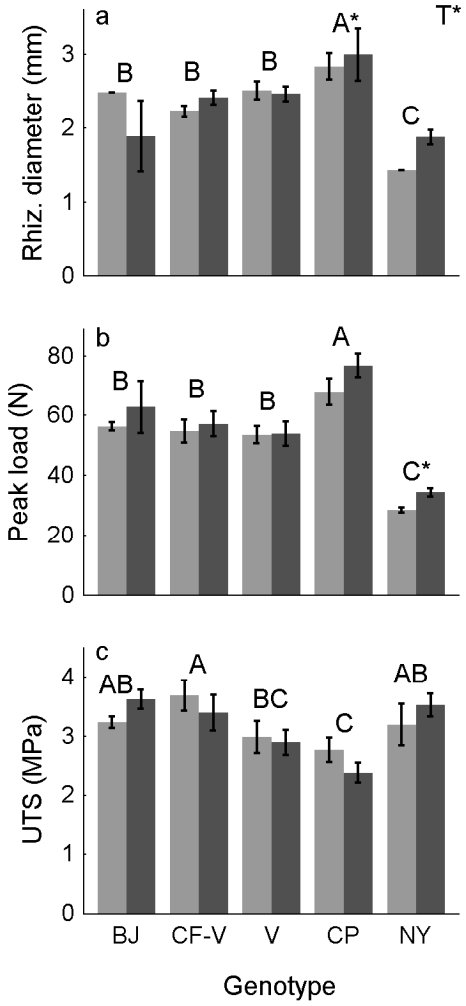

Fig. 2.2 Differences in traits related to tensile strength (mean ± SE) among genotypes after 28 weeks of growth under control and elevated nitrate treatments; for (a) *Rhizome diameter (*genotype effect: $F_4 = 26.35$, $P < 0.001$, $\eta^2 = 0.65$; nutrient effect: $F_1 = 4.48$, $P = 0.04$; $\eta^2 = 0.07$); (b) *Peak load* (genotype effect: $F_4 = 16.94$, $P < 0.001$, $\eta^2 = 0.55$; nutrient effect: $F_1 = 2.64$, $P = 0.11$); (c) *Ultimate tensile strength* (genotype effect: $F_4 = 5.28$, $P = 0.001$, $\eta^2 = 0.28$; nutrient effect: $F_1 = 0.00$, $P = 0.95$) . At the top right of each panel, T* indicates nutrient effect $P < 0.05$; above bars, * indicates genotypes with a significant nutrient effect, letters indicate significant pairwise differences among genotypes

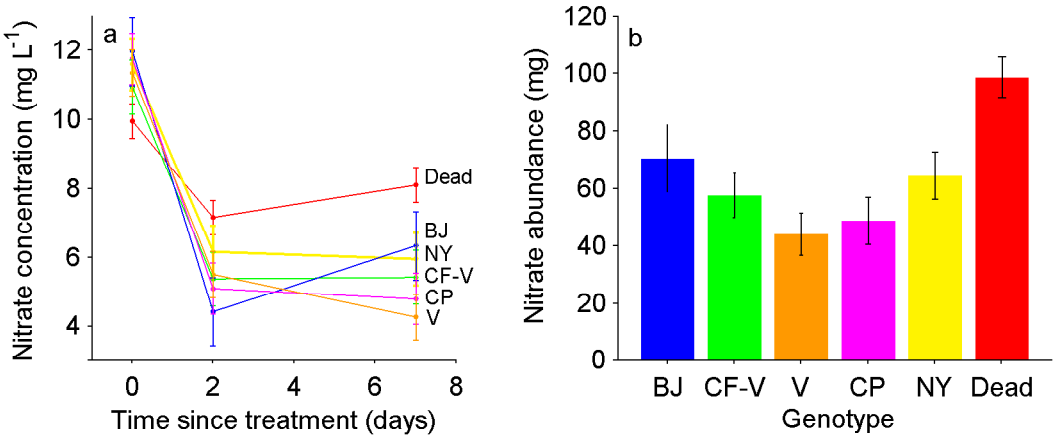

Fig. 2.3 Genotypic differences (mean ± SE) following nutrient addition; in (a) groundwater *nitrate* (NO_3^-) *concentrations* over time and (b) final groundwater *nitrate abundance* after week

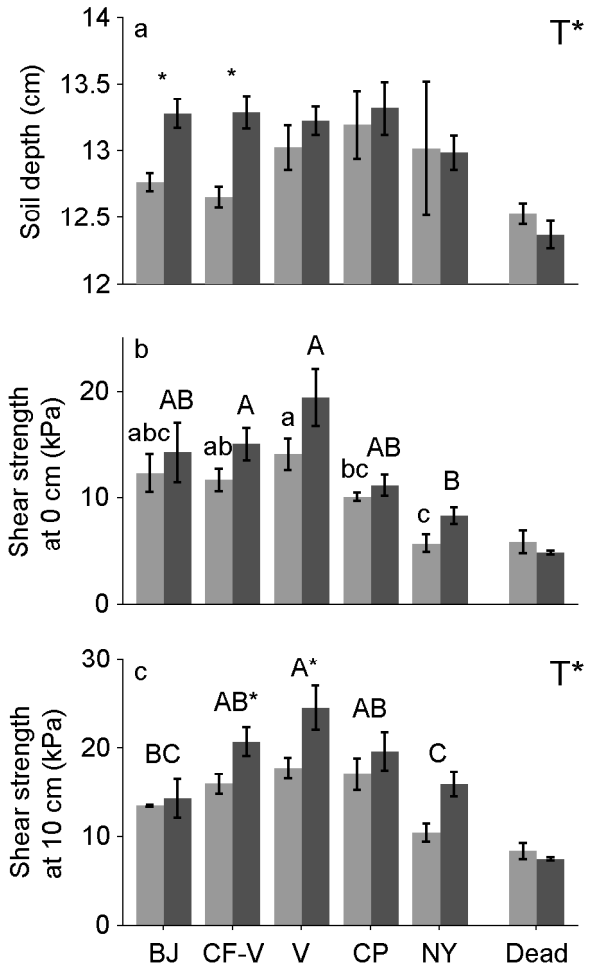

Fig. 2.4 Genotypic differences (mean ± SE) in proxy measures of erosion-buffering engineering activities after 28 weeks of growth under control and elevated nitrate treatments; for (a) *soil depth* (genotype effect: $F_4 = 0.99$, $P = 0.42$, η^2; nutrient effect: $F_1 = 4.93$, $P = 0.03$, $\eta^2 = 0.08$); (b) *soil shear strength* (0 cm) (genotype effect within controls: $K_4 = 10.13$, $P = 0.04$; genotype effect within the elevated nutrient treatment: $K_4 = 13.73$, $P = 0.01$; nutrient effect: $K_1 = 1.14$, $P = 0.29$); (c) *shear strength* (10 cm) (genotype effect: $F_4 = 3.92$, $P = 0.007$, $\eta^2 = 0.21$; nutrient effect: $F_1 = 7.17$, $P = 0.01$, $\eta^2 = 0.11$). At the top right of each panel, T* indicates treatment effect $P < 0.05$; above bars,

* indicates a significant nutrient effect, letters indicate significant pairwise differences among genotypes

CHAPTER 3: SHORELINE EROSION VARIES ACCORDING TO SPATIAL HETEROGENEITY IN COASTAL MARSHES

3.1 ABSTRACT

Salt marsh ecosystems are eroding at an unprecedented rate around the globe, yet the factors driving shoreline retreat remain poorly understood. Materials research investigating similar processes suggests that spatial heterogeneity in resistance may affect characteristics such as the position, speed, and profile of erosion fronts. Using a modelling approach, we perform mean field analyses and cellular automata simulations to examine how the presence and distribution of spatial heterogeneity affects shoreline erosion. Because soil resistance is likely to vary over the same spatial scale as the vegetative engineering activities it is shaped by, we tested the effects of autocorrelation over distances corresponding to different vegetative clone sizes. Models were parameterized with high resolution data on soil shear strength and erosion rates, then used to generate explicit predictions. We found that erosion accelerated in response to increased variance of soil shear strength values. This was primarily due to the nonlinear relationship between erosion and soil shear strength, but also because shoreline geometry became increasingly complex. Autocorrelation strengthened these effects, giving rise to intervals of comparatively low and high erosion. Autocorrelation also altered the scale of front mobility and the probability of mass failure events, accelerating erosion by a diminishing amount as it increased. Wave power magnified the effects of heterogeneity, but did not otherwise alter them. These results indicate that a large amount of variation in shoreline-scale erosion processes may be overlooked by discounting heterogeneity and

spatial patterning. Our findings also suggest possible improvements to coastal management approaches. Diagnostic landform features resulting under varying autocorrelation distances may help improve erosion monitoring efforts by providing a preliminary indication of erosion fronts influenced by spatial heterogeneity.

3.2 INTRODUCTION

Global loss of valued salt marsh ecosystems has been accelerating with increasing natural and anthropogenic subsidence, inundation, and erosion [96, 97, 98, 99]. The success of efforts to stem further loss and to restore salt marshes will depend on understanding ecosystem responses to stressor conditions such as wind-wave forces. Numerical mechanistic models have been developed to provide predictive frameworks for understanding forcings and feedbacks in marsh ecosystems, including processes that govern elevation in equilibrium with sea-level and determine vertical marsh loss [18]. Progress has been made with characterizing erosional processes that can drive salt marsh loss, but it is not clear how biogeomorphic interactions influence the lateral retreat of shorelines under wind-wave forces (e.g., [100, 101, 102, 103, 104, 105]). Variation in alongshore erosion has been attributed to heterogeneity in marsh properties shaped by biogeomorphic interactions [105, 106]. In addition, there is mounting evidence that the spatial grain of heterogeneity can have emergent effects on how fronts propagate through composite media [107, 108, 109]. Nonetheless, investigation of the influence of spatial heterogeneity on the propagation of erosional fronts is only just commencing [110, 111], as predictive models of shoreline erosion have typically assumed that marsh characteristics are constant [105, 106].

Foundational plants are central to biogeomorphic and landform dynamics in salt marshes [18, 112], and thus represent a likely source of spatial variation in erosion resistance. Landform engineers, like *Spartina alterniflora* (smooth cordgrass), that dominate coastal marshes can greatly increase soil shear strength, which largely determines susceptibility to erosion [13, 15, 113]. Common garden field experiments also have demonstrated that shoreline erosion rates can differ according to heritable phenotypic variation in *S. alterniflora* [71]. This suggests that rates of erosion may reflect the distribution and grain of intraspecific variation in plant traits, particularly engineering traits that modify soil shear strength, such as belowground biomass and rhizome thickness [71, 114]. It further suggests that variability in clone size could influence how erosion propagates from a shoreline. Grasses such as *S. alterniflora* can vegetatively reproduce via radially expanding rhizomes, giving rise to dense circular clones that can span tens or even hundreds of meters in diameter [115]. Clonal patches may generate a mosaic pattern of engineer trait variation and autocorrelated erosion resistance. By contributing to non-random heterogeneity, the spatial organization of clonal patches may influence transitions between states with varying stability [116], allowing plant community composition to mediate the pace and scale of erosion events.

Here, we develop a cellular automata (CA) model to examine the relationship between wave-driven erosion and spatial variation in soil shear strength reflecting intraspecific variation and clonal patch size. We use high resolution spatial erosion data to parameterize our model, supplemented with regional measures of wind and wave characteristics. Through simulations, we estimate and compare erosion rates, year-to-year variability, and shoreline shape under conditions of increasing variance of local soil shear

strength and increasing autocorrelation. By parameterizing the model with empirical estimates of shoreline erosion, we also illustrate the range of potential outcomes of conditions observed in field studies. Doing so afforded broader perspectives on relationships and factors governing erosion, building on principles derived from conceptual models and empirical predictions.

3.3 MATERIALS & METHODS

Model theory

To build a model that does not rely on underlying conceptual assumptions, we began with a spatially implicit formulation based on first principles of dimensional relationships between marsh erosion properties, following Marani et al. [30]:

$$\frac{Rhc}{\bar{P}_I} = f\left(\frac{h}{d}\right) \quad (1)$$

where R is erosion rate (in m yr^{-1}), $\bar{P}_I$ is mean wave power density upon impact (in Wm^{-1}), and $f(\,)$ is a function relating h, the height of the marsh cliff face above the tidal flat bottom (in m), with d, the depth of the tidal flat bottom with respect to sea level (in m). The parameter c represents erosion resistance (e.g., soil shear strength, in Pa), which encompasses the positive effect of plant growth. For a given site, Marani et al. [30] showed that $Rh/\bar{P}_I$ was independent from h/d, so that if constant c was assumed, $f(h/d)/c$ could be taken as approximately constant:

$$f(h/d)/c \cong a \quad (2)$$

Simplification gives the following proportionality:

$$R \cdot h = a\bar{P}_I \quad (3)$$

which is well supported by empirical observations [30]. Alternative marsh erosion models have used *ad hoc* approaches to relate R and P_I using a non-linear formulations, most commonly a power law:

$$R = \frac{a}{h}\bar{P}_I^{\,b} \tag{4}$$

where b is a site-specific empirical constant, and constant h is assumed [102, 110, 111, 117]. However, within the range of empirical observations, Marani *et al*. [30] showed that results of Eq. 4 do not significantly differ from those predicted by Eq. 3.

While Eq. 3 offers robust predictive capacity across marshes, within-site applications are characterized by large unexplained variation. The response of R to changes in $\bar{P}_I$ is strongly dependent on the value of c, allowing the potential for large error if a single marsh captures some portion of the wide range of c values observed across sites [30]. To consider the influence of variable soil strength on R, our simplification of Eq. 1 retains c and specifies its position within the marsh. Linearity between R and $\bar{P}_I$ has been observed within sites when constant h is assumed [30, 102, 117, 118], allowing us to use the formulation:

$$R_{(x,y)} = \frac{\varphi \bar{P}_I}{c_{(x,y)}} \tag{5}$$

where (x, y) is a position within the marsh and $\varphi \equiv f(h/d)/h$ is introduced to represent a site-specific constant.

For spatial scales on the order of a kilometer or less, it is reasonable to assume that the strength and direction of wave power density prior to impact, $\vec{\boldsymbol{P}}$**,** are uniform. Because of the shoreline curvature, however, wave power density upon impact at location

(x, y) will depend on $\alpha_{(x,y)}$, the angle of approaching waves relative to shore-normal. This relationship can be described by:

$$\bar{P}_{I,(x,y)} = \overline{\left|\vec{\boldsymbol{P}}\right| \cos \alpha_{(x,y)}} \tag{6}$$

where vector $\vec{\boldsymbol{P}}$ is wave power density prior to impact and $\alpha_{(x,y)}$ is the angle of $\vec{\boldsymbol{P}}$ relative to shore-normal at position (x, y) [30].

We used a mean field approach to identify the effect of the variance of soil shear strength on shoreline erosion rates when spatial effects were excluded. Based on scale transition theory [119, 120], we obtained the following mean field approximation from Eq. 5:

$$\bar{R} = \frac{\varphi \bar{P}_I}{\bar{c}} + \sigma_c^2 \frac{\varphi \bar{P}_I}{\bar{c}^3} \tag{7}$$

where $\bar{R}$ is the average rate of shoreline erosion, $\bar{c}$ is the average soil shear strength, and σ_c^2 is the variance of c.

Empirical support and parameterization

Data on soil shear strength and erosion rates at different positions along a shoreline was used to evaluate the predictive ability of Eq. 5 and to obtain a parameter estimate representing a highly erosional salt marsh site. Soil shear strength and erosion measures were obtained from a field-scale revegetation experiment in Bay Jimmy, LA [25, 71].

Because the direction and magnitude of $\vec{\boldsymbol{P}}$ vary independently over time according to wind conditions, we used NOAA buoy station GISL1 data on wind direction and speed over the study period to identify a suitably weighted average over time:

$$\bar{P}_{I,(x,y)} = \bar{P} \cdot \overline{\cos \alpha_{(x,y)}} = \bar{P} \cdot \sum w_\beta \cos \alpha_{\beta,(x,y)} , \qquad \text{for } 0 \leq \frac{\beta}{45^\circ} \leq 8 \tag{8}$$

where β is wind direction, w_β is a normalized weight, and $\bar{P}$ is average $\left|\overrightarrow{\boldsymbol{P}}\right|$ over time. Plotting $R_{(x,y)}/\overline{\cos\alpha_{(x,y)}}$ against $1/c_{(x,y)}$ and fitting Eq. 5 yielded an approximation for the constant term $\varphi\bar{P}$.

Spatially explicit simulations

To examine the spatial effects of heterogeneity over different levels of autocorrelation, we incorporated a parameterized version of Eq. 5 into a stochastic CA model. Space was structured as a rectangular, square-tiled lattice of 256 x 256 elements, each representing one square meter occupied by marsh or water. Marsh cells with sides bordering both water and land compose the marsh edge, and convert to water with probability:

$$p_{i,\Delta t} = \frac{R_i}{\sum_{j=1}^{n} R_{i,j}} \tag{9}$$

where R_i is given by Eq. 5, j designates a cell on the marsh edge, n is the total number of edge cells, and Δt is the time interval.

The model incorporates natural variation in wind conditions by assuming β is equally distributed across three sequential multiples of 45°, which give an average $\overrightarrow{\boldsymbol{P}}$ that is normal to the initial shoreline. Different sides of a cell receive different fractions of $\bar{P}_{I.i}$ according to Eq. 6, causing p_i to increase as more sides become exposed. At the end of an iteration, cells or groups of cells that are surrounded by water on all sides automatically erode to mimic mass failure or sinking marsh islands (following [110]).

Analyses

We first assessed the influence of shoreline geometry on erosion rates over time. Assuming marsh properties are uniform and P is constant, a straight shoreline edge with

length L will lose area at a rate $R \cdot L$, causing cumulative erosion to increase linearly over time. However, the erosion of discrete cells over successive time steps may increase the roughness of the shoreline, exposing a greater number of edge cells as L increases. To assess the importance of this effect on erosion rates over time, we compared the constant rate predicted by Eq. 3 to rates simulated over time according to the spatially explicit model. We then relaxed the assumption of uniform resistance to erosion. To examine how erosion rates are affected by different levels of variance in the soil shear strength c, simulations were used to examine long-term average erosion rates, the variability of erosion rates over time, and the final shape of the shoreline after 50% of the cells had eroded. The roughness of the shoreline was measured as the root mean square distance between shoreline cells the mean profile position, and we refer to the total length of the shoreline relative to its roughness as shoreline complexity. To examine how autocorrelation influences erosion, we repeated the comparisons with variation distributed into different clonal patches: 5, 50, 100, 500, and 1000 m^2. Simulations were run under the wave power density observed in the field (1 P), and repeated for wave power adjusted by a factor of 0.1, 0.5, 1.5, and 5.0.

3.4 RESULTS

Model performance

The first principles-based formulation (Eq. 5) provided a good fit for erosion data plotted against corresponding soil shear strength ($R^2 = 0.55$), with nearly all points falling within the 95% confidence interval (CI) using the estimated parameter $\varphi \cdot \bar{P}_{I,i} = 22.01 \pm 5.23$ (Fig. 3.1). Simulated erosion rates for marshes with uniform soil shear strength were

slightly higher than those predicted by Eq. 5, but well within the 95% CI ($R^2 = 0.95$; Fig. 3.1).

Erosion rates for random heterogeneity under varying wave power

As mean soil shear strength increased, erosion rate decreased exponentially (Fig. 3.2). Applying the equation derived by scale transition theory (Eq. 7) showed that erosion rate increased exponentially as the standard deviation of soil shear strength increased, though the effect size was small over a range of realistic soil shear values (Fig. 3.2). While variation had a larger effect on erosion when mean soil shear strength was low, lower mean values also limited the magnitude of potential variation (Fig. 3.1). Under observed wave power conditions, heterogeneity in soil shear strength increased erosion rates by a maximum of 33% compared to uniformly distributed soil shear strength (Fig. 3.1). The positive linear effect of wave power on erosion slowly increased in strength as heterogeneity increased (Fig. 3.2). As increasing wave power increased erosion rates, differences between heterogeneous and uniform conditions became amplified (Fig. 3.2). Similarly, simulated erosion rates under heterogeneous conditions became increasingly greater than predictions based on scale transition (Eqn. 7) as predictions increased (Fig. 3.2).

Erosion rates for autocorrelated heterogeneity under varying wave power

Erosion rates increased logarithmically with increasing clone size (Fig. 3.3). Under observed wave power conditions, contributions of clone size to heterogeneity elevated erosion ≤11%. The relationship plateaued when clone size reached 100 m^2. The effect of

the wave power on erosion rates increased in strength with increasing clone size until 100 m^2, after which increasing clone size weakened the strength of the effect (Fig 2c). Increasing wave power also amplified differences in erosion rates for different clone sizes (Fig. 3.3).

Temporal variation in erosion rates

The variability of annual erosion rates increased exponentially with increasing spatial heterogeneity (Fig. 3.4). Within the range of observed wave power, temporal variation in erosion rates was 24% higher under conditions of high spatial heterogeneity (s = 6) versus uniformity. When heterogeneity was organized into clonal patches, increasing clone size increased temporal variation in erosion rate logarithmically, such that 100 m^2 clones had 98% higher temporal variation in erosion compared to conditions of random spatial heterogeneity within the range of observed wave power (Fig. 3.4). More specifically, as clone size increased, periods of exceptionally high erosion became more common, creating increasing rightward skew in the frequency distribution of erosion rates (Figures 3.5 & 3.6). This skew persisted as variation in erosion rates increased under increasing wave power (Figures 3.5 & 3.6). For a given spatial configuration, increasing wave power caused the coefficient of variation (CV) for annual erosion rates to decrease exponentially.

Random variation and spatially organized variation in soil shear strength increased shoreline roughness under erosional conditions (Fig. 3.7). Shoreline roughness significantly increased as the standard deviation of soil shear strength increased from 3.0 to 6.0 kPa ($t_4 = 3.75$, $p = 0.02$), rising from an average of 24.8 to 29.6, compared to

s = 18.4 for uniform conditions. By comparison, average roughness measured 38.1 for the smallest clone size (5 m^2) and increased logarithmically with increasing clone area - up to 236.6 for 100 m^2 clones, and nearly 500 as clone sizes surpassed 1000 m^2. Notably, wave power had no effect on shoreline roughness.

3.5 DISCUSSION

By adapting a first-principles model, we show how erosion rates and shoreline evolution can vary according the extent and spatial distribution of heterogeneity in soil shear strength. Parameterization of our model demonstrated that the relationship between soil shear strength and erosion holds for plot-scale measures (25 m^2) taken along a single shoreline, though the data was characterized by a large amount of scatter. Results from simulations indicate that, when holding mean soil shear strength constant for a site, local heterogeneity can accelerate shoreline erosion. The effect of local heterogeneity increased sharply when it was nonrandomly distributed; spatial autocorrelation not only increased long term erosion rates, it also increased year-to-year variability in erosion and shoreline roughness.

The effects of random heterogeneity on erosion under the CA model provided broad agreement with our mean-field treatment of the problem, but also demonstrated a spatial interaction. Because scale transition theory accounts for the majority of the observed erosional responses, we can infer that the effect of random heterogeneity is primarily due to the nonlinear relationship between erosion and soil shear strength. Accordingly, as the variance of shear strength increases, erosion accelerates more for lower values than it decelerates for higher values. Our mean field formulation did not

account for the full amount of simulated erosion, however, indicating an additional spatial component to the response. We found that the difference between models was fully explained by changes in shoreline length. In our CA model, erosion along lateral planes exposed the marsh to transverse erosion, which in turn could increase the complexity of its shape. This process accelerated erosion rates by increasing the area of marsh susceptible to erosion. Thus, the effect of heterogeneity on erosion rates may also depend on how it effects shoreline geometry.

Our results indicate that spatial autocorrelation can accelerate erosion in heterogeneous marshes through several mechanisms and interactions with shoreline geometry. The area of shoreline that the strongest or weakest soils are likely to occupy at any one time increases when soil strengths are spatially aggregated. This increases the frequency of exceptionally high and low short-term erosion rates, and increases the difference in erosion between the two extremes. Successive erosion into large areas of weak soil allows shoreline geometry to rapidly increase in complexity, which accelerates erosion rates by lengthening the shoreline This can encourage further loss through mass failure of resistant shoreline projections due to erosion of weak linkages. Through interactions with shoreline geometry, the effects of these mechanisms diminish as autocorrelation distance increases: as uniform patches increase in relative size, progressively fewer transitional boundaries occur between areas with different soil shear strength, decreasing complexity. This exponentially reduces shoreline lengthening as autocorrelation distance increases, until it reaches an asymptotic maximum. Consequently, increasing autocorrelation has diminishing effects.

Inconsistencies between our findings and those of other models illustrate the merits of our approach for understanding erosion in salt marshes. For example, Leonardi and Fagherazzi [110, 111] found that spatial heterogeneity did not affect average erosion rates and that it only increases temporal variability in erosion under low wave power. Unlike prior models, however, our model accounts for directional variation in waves, and the cumulative effects of directional variation on all exposed sides of a cell. More importantly, however, we also do not assume that soil shear strength acts as a maximum threshold above which erosion cannot be resisted, such that its effect on erosion approaches zero as wave power increases. This is represented by a rational shear strength term that is in exponentially inverse proportion to erosion:

$$R_i = aP^b e^{-\frac{c_i}{f(P)}} \quad (10)$$

where $f(P)$ can increase as a function of wave power density to attain values greater than the threshold soil shear strength, c_i [110, 111]. Yet, wave shear stress in salt marshes does not appear to exceed these thresholds, even during extreme storm events [15]. For example, Hurricane Katrina generated enough shear to induce erosion for strengths up to 1.8 kPa (per 1 m^3, incorporating 1 m root depth), while the lowest recorded thresholds range from 2 - 4.5 kPa [15, 111] and are typically in excess of 10 kPa [15, 71]. This suggests that salt marsh erosion corresponds to progressive failure under the repeated and cumulative forcing of waves, as soil instability and rootmat degradation increase in inverse proportion to soil strength [113, 121]. Models assuming threshold behavior thus are likely more applicable to brackish marshes that exhibit comparatively weaker soils [15].

Though regularly spaced cusps of land can form in coastal systems through other self-organizing physical processes, the size and shape of projections in salt marshes often approximate visible clonal boundaries. The size and shape of projections in salt marshes often approximate visible clonal boundaries (Figures 3.8 & 3.9), and at sites where previous studies [115] have determined differences in the size and number of *S. alterniflora* clones, satellite images reveal differences in shoreline geometry that are consistent with the results of our model. For instance, at sites where Travis and Hester [115] reported higher clonal autocorrelation distances, simulated shorelines exhibit larger-scale transverse concavities and projections, while smaller-scale projections consisting of smaller clones bare a close resemblance to predictions of more complex shorelines (Figures 3.8 & 3.9). Though further work will be necessary to validate initial predictions, this raises the possibility that our model could be a tool for inferring the demography of clonal salt marsh plants from diagnostic shoreline features.

The results of our study indicate that consideration to a few key factors could improve the success of shoreline restoration and accuracy of erosion measurements. Salt marsh restoration projects predominantly employ *S. alterniflora* cultivars, and an increasing number of cultivars are being developed to promote genetic diversity in restored marshes. Our findings suggest that plant stocks should be selected based on differences in engineering abilities. For example, it is important to consider both the mean and variation in soil strength that cultivars may confer. In addition, minimizing the planting distance between individuals could minimize autocorrelation. Our results further illustrate that the accuracy of estimated erosion rates can vary widely depending on the timescale of measurements, which affirms that studies of shoreline erosion should

account for short and long-term (e.g., year-to-year) variability. Comparisons intended to characterize loss (e.g., from oil spills and storm events) should also account for differences in spatial heterogeneity between impacted and reference sites. Consideration to shoreline shape could provide a useful preliminary indication of sites where heterogeneity has a large influence on erosion.

With further refinement, our model might prove useful for characterizing outcomes of marsh restoration or shoreline remediation. For example, by incorporating drivers of plant demography, it might be possible to simulate shoreline stability and evolution according to different restoration strategies. Changing interactions among plants and the environment could result in novel erosion dynamics by generating more complex patterns of nonrandom spatial variation than what we have so far considered. For example, the fitness of plants with different shear strengths may be influenced by shoreline geometry, where population responses to wind-wave exposure govern the organization and distribution of spatial heterogeneity. This also raises the possibility that understanding of erosional processes could be improved by considering whether patterns of spatial variation might emerge from ecological and evolutionary feedbacks

3.6 FIGURES

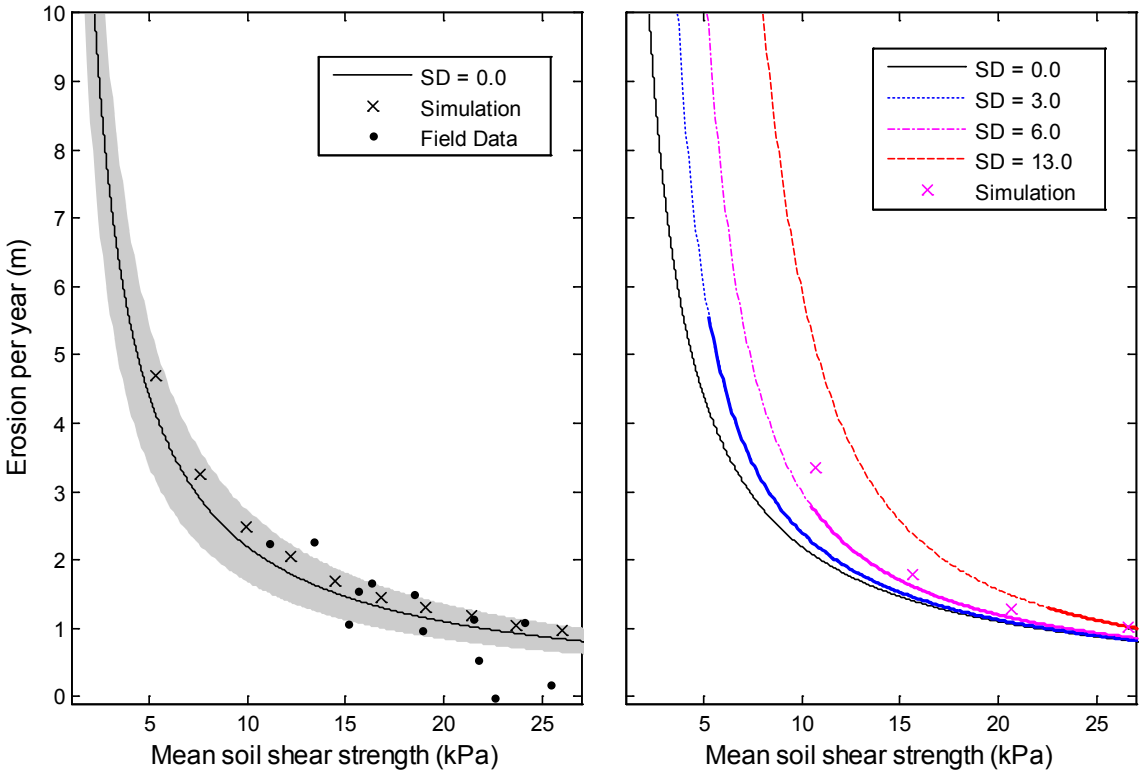

Fig. 3.1 Erosion as a function of soil shear strength, showing (a) field data from a site in Bay Jimmy (LA, USA) falls largely within the shaded 95% confidence interval of predicted values ($R^2 = 0.55$), and model simulations closely approximate predictions ($R^2 = 0.95$); (b) erosion predicted for heterogeneous marshes using the parameterized scale transition equation. The standard deviation of soil shear strength ranges from SD = 0.0 to SD = 13.0. As soil shear strength must be positive, the possible mean values are represented by the solid portion of each line. Simulation results are compared for SD = 6.0

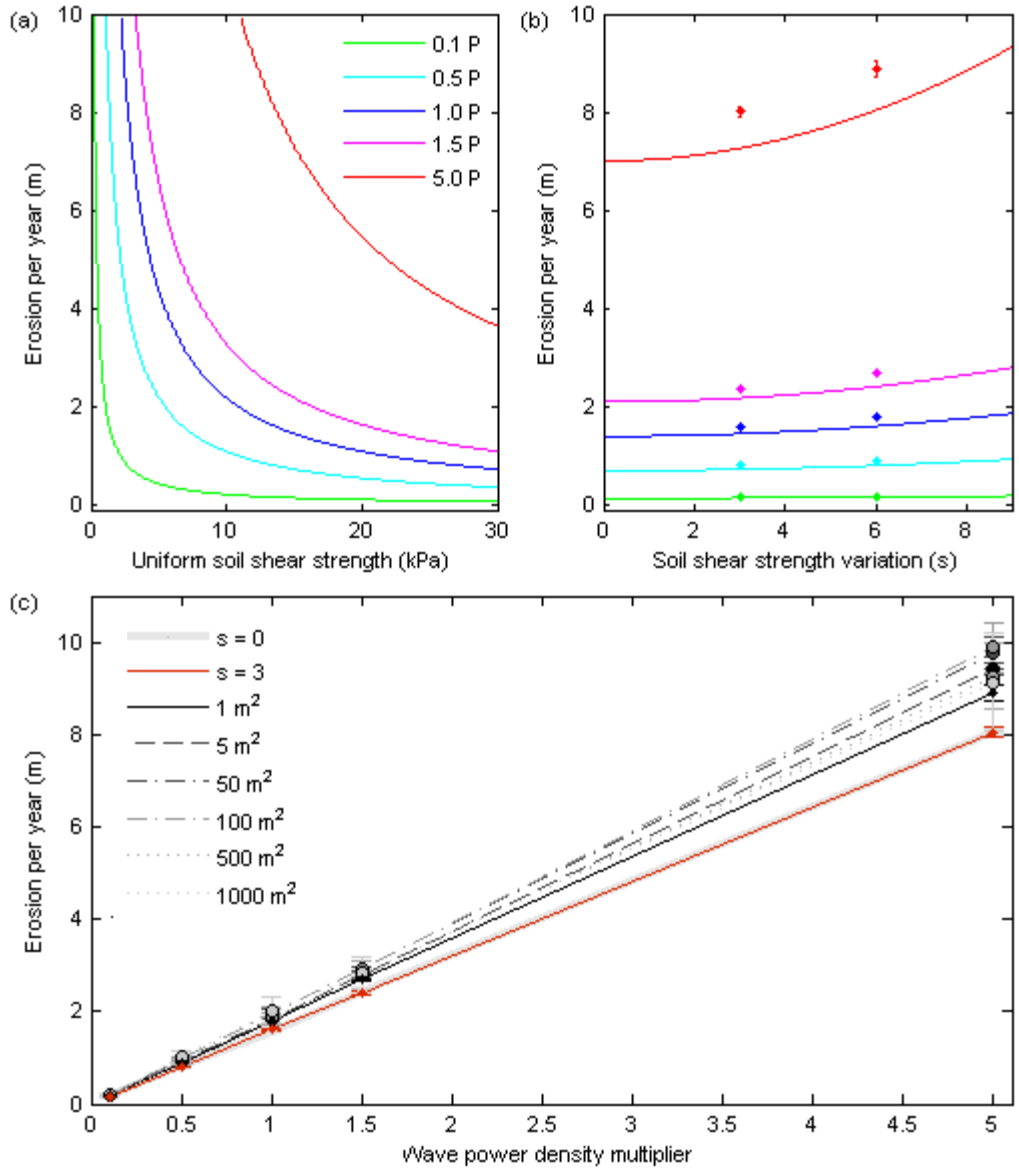

Fig. 3.2 (a) The predicted relationship between erosion rates and soil strength under different levels of wave power density (*P*) for homogeneous marshes; (b) mean field erosion rate predictions as soil strength variance increases, for different levels of *P*; points depict simulation results for $s = 3$ and $s = 6$; (c) the relationship between erosion and *P* for different levels of variance (solid lines), and increasing clone sizes (broken lines)

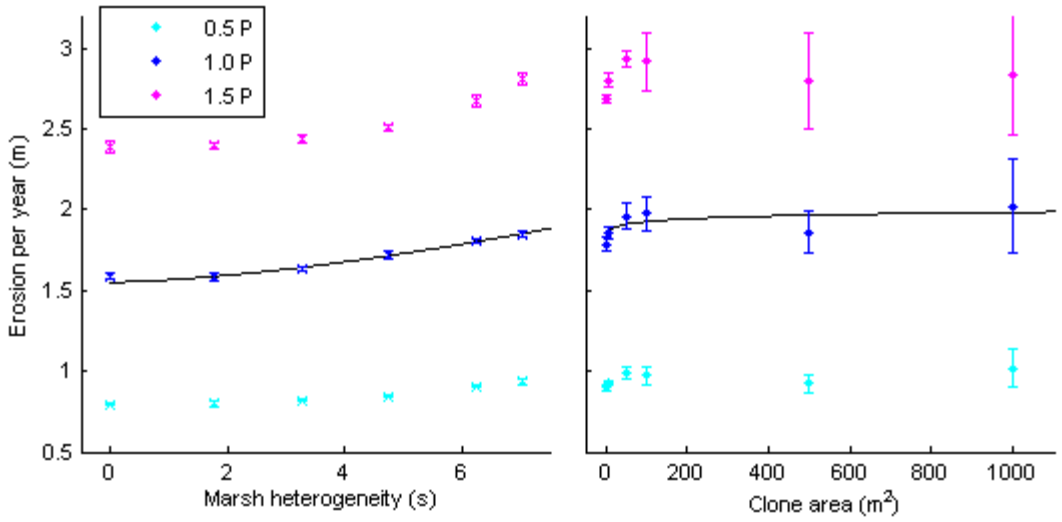

Fig. 3.3 The relationship between simulated erosion rates and the variance of soil shear strength values under different levels of wave power density (*P*) (left), and the relationship between simulated erosion rates and autocorrelation distance (i.e., clone size) (right)

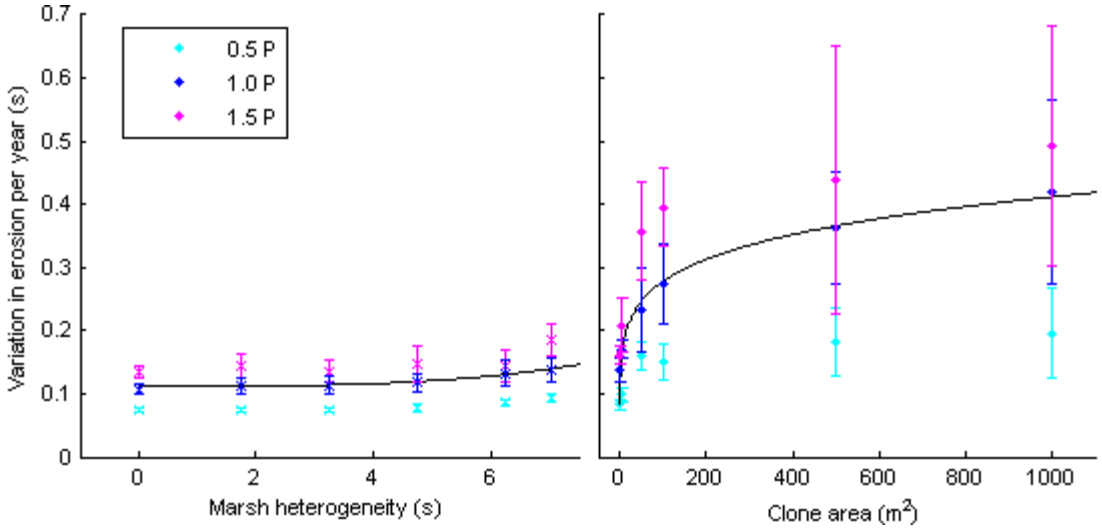

Fig. 3.4 The relationship between the variability of simulated annual erosion rates and the variance of soil shear strength values under different levels of wave power density (*P*) (left), and the relationship between the variability of simulated annual erosion rates and autocorrelation distance (i.e., clone size) (right)

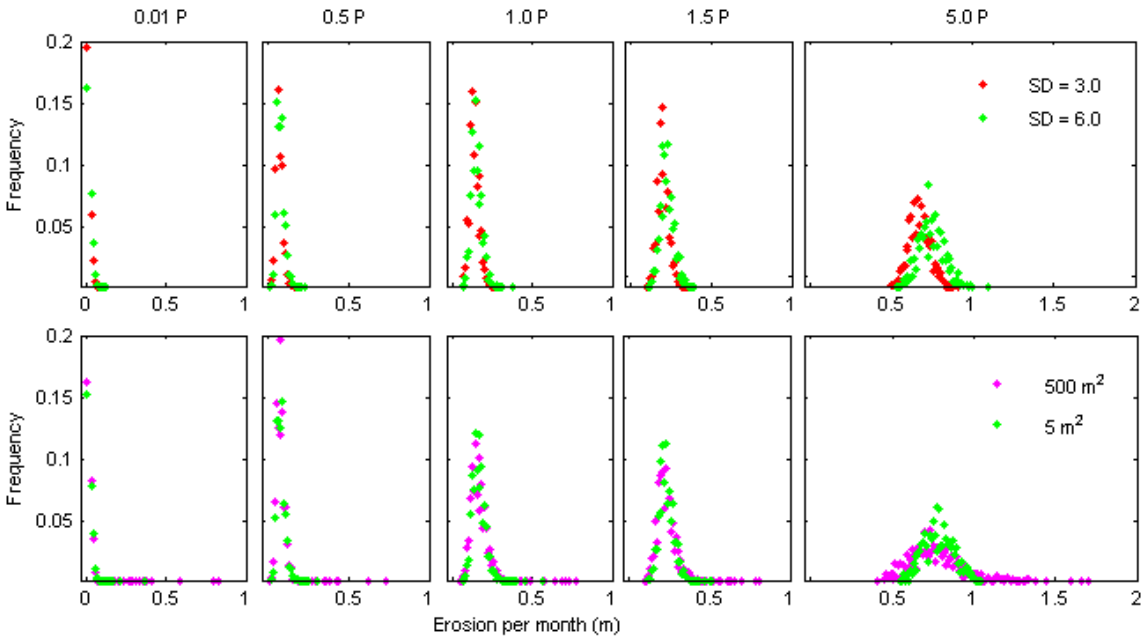

Fig. 3.5 The frequency distribution of monthly erosion rates over all months and all replicate simulations, compared for high and low soil shear variance (top panel) and large and small autocorrelation distances (bottom panel), over increasing wave power density (*P*)

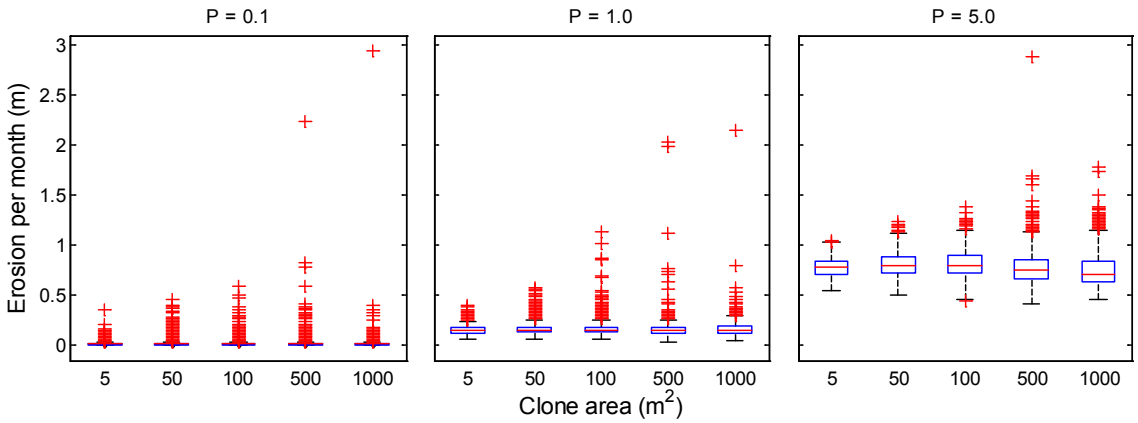

Fig. 3.6 The distribution of monthly erosion rates (over all months and all replicate simulations) for increasing autocorrelation distances (i.e., clone sizes), over increasing wave power density (*P*)

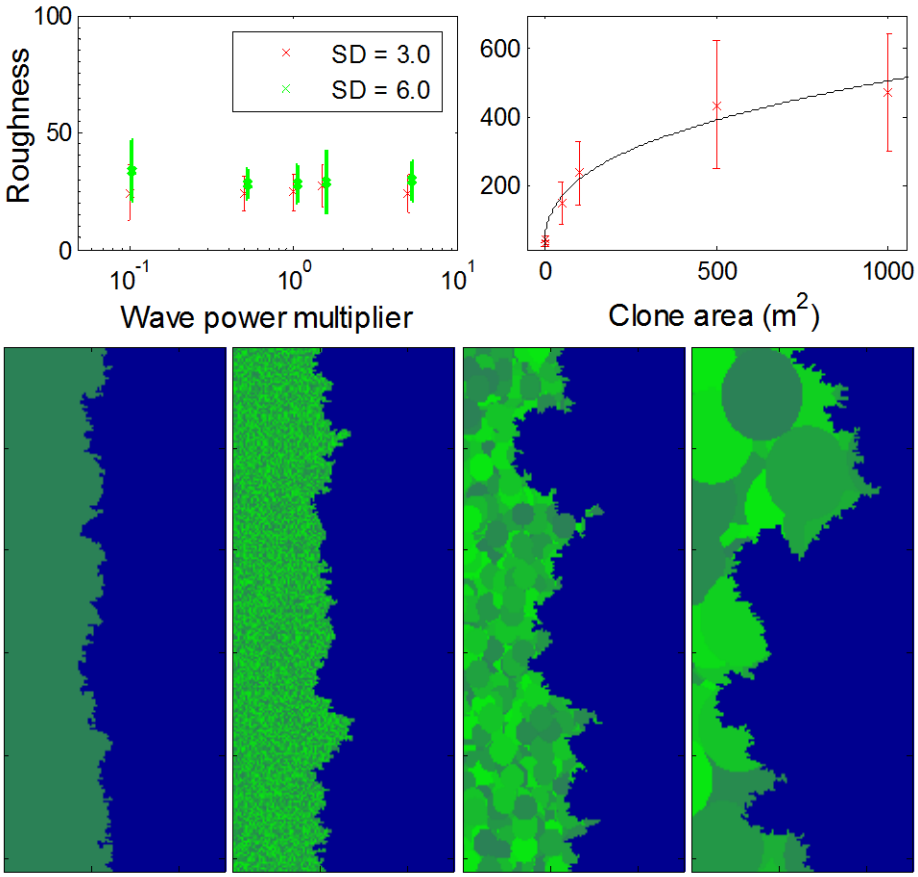

Fig. 3.7 The effect of soil shear strength variance (top left) and autocorrelation distance (i.e., clone area) (top right) on shoreline roughness. The final shoreline lattices are depicted for sizes measuring $1m^2$, $5m^2$, $20m^2$, and $500m^2$ (bottom panel)

Fig. 3.8 Eastern shoreline shapes for marshes with large and small clone sizes. Marsh Island (left) and the Breton Sound (center) clone diameters measured at least 30 m on average, ranging as high as 119 m and 593 m respectively. Clone diameter at Sabine Refuge (right) was less than 10 m on average, with a maximum measure of 14 m, and the shoreline features were comparatively reduced in size. Shear stress arrives predominantly from the southwest. All images are to scale

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Fig. 3.9 Southern shoreline shapes for marshes with varying clone sizes. Maximum clone diameter at Sabine Refuge (top left) was 14 m, while the average was less than 10 m. Marsh Island (bottom left) clone diameters measured at least 30 m on average, ranging as high as 119, and the shoreline was comparatively rougher (both images are to scale). Interior and shoreline clone perimeters are distinguishable along a broader stretch of the Marsh Island shoreline (right)

APPENDICES

APPENDIX 1: MICROSATELLITE GENOTYPE DATA COLLECTION, ANALYSIS, AND RESULTS

Microsatellite genotype data collection and analysis

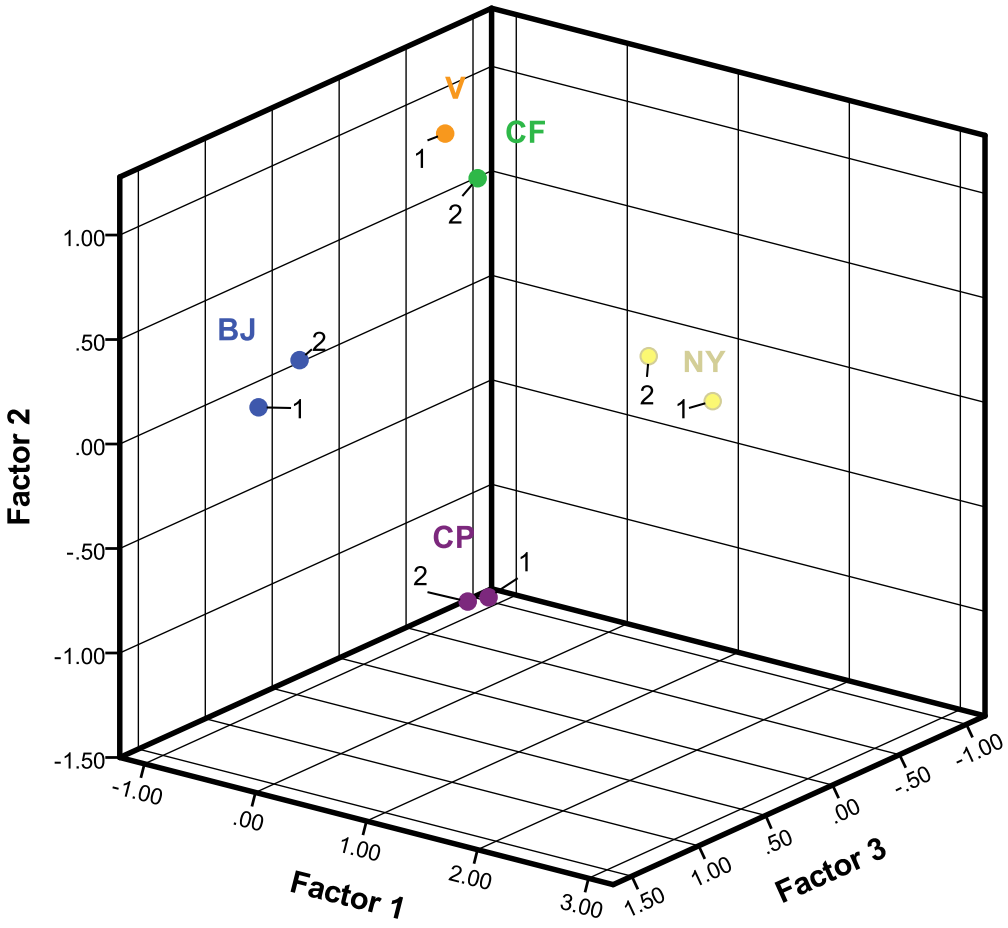
For each plot, three green leaf tissue samples (taken from one of the plug locations) were collected for microsatellite genotyping to confirm genotype identity and variability among treatments planted from different source populations. DNA was extracted from each sample using a DNEasy plant extraction kit. Samples were genotyped at 9 microsatellite loci: SPAR3, SPAR5, SPAR7, SPAR8, SPAR13, SPAR14, SPAR16, SPAR18, and SPAR20 [52, 53]. Approximately 10–50 ng of genomic DNA was used as template in 15 µl PCR mixtures that included 1.0 mM MgCl2, 166.67 µM each dNTP, 0.5 U hot-start *Taq* DNA polymerase (MCLAB, San Francisco, California, USA), 1x PCR buffer (MCLAB), 1 µM each primer, and H_2O added to attain the final volume. Forward primers were fluorescently labeled with HEX, 6-FAM, or NED. Amplified products were generated using Eppendorf thermal cyclers (Eppendorf Internation, Hamburg, Germany) programmed to run one cycle at 95˚C for 10 minutes, 35 cycles at 94˚C for 45 seconds, the primer-specific annealing temperature for 30 seconds, and 72˚C for 90 seconds, followed by a final extension stage at 72˚C for 5 minutes. Fragment sizes were determined against a GeneScan 600 LIZ standard (Applied Biosystems Inc., Carlsbad, California, USA) using an ABI 3730xl DNA Analyzer. Electrophoretic output was scored with GeneMarker® software (Soft Genetics LLC, State College,

Pennsylvania, USA). GENALEX v.6.5 was used to identify multilocus matches among genotyped individuals [54] and to calculate genotypic richness (G), the absolute number of different genotypes, for each plot and for each genotype treatment. To examine genetic variation among planted treatments, ARLEQUIN v. 3.5 was used to calculate pairwise values of F_{ST}, and to compute the log-likelihood of assigning each individual genotype to other treatments [55].

Genetic and genotypic variation

Genotypic diversity in natural source populations was bracketed by contrasting high and low levels found in cultivar source populations. Among cultivar treatments, a single genotype was recovered from V plots, with one exception, indicating that the genetic stock supplied by nurseries approached monoculture conditions (Table 1). By contrast, the experimental CP plots consisted of several distinct genotypes, with only one genotype shared by two samples, suggesting that the CP experimental line is a result of mixed ancestry. The natural population treatments exhibited comparable genotypic richness, both overall and among plots (Table 1). Though some differences in genotypic richness were observed among natural source treatment plots, samples in some plots shared a single genotype, and both the BJ and CFL treatments exhibited genotypes that occurred across multiple plots. All genotypes were correctly assigned to the corresponding treatment according to likelihood values. Pairwise distance values (F_{ST}) among treatments ranged from 0.02 to 0.10. Differentiation was not significant for any pair based on permutations of individuals between populations, which likely reflects the limitations of estimating genetic distance for small sample sizes [56].

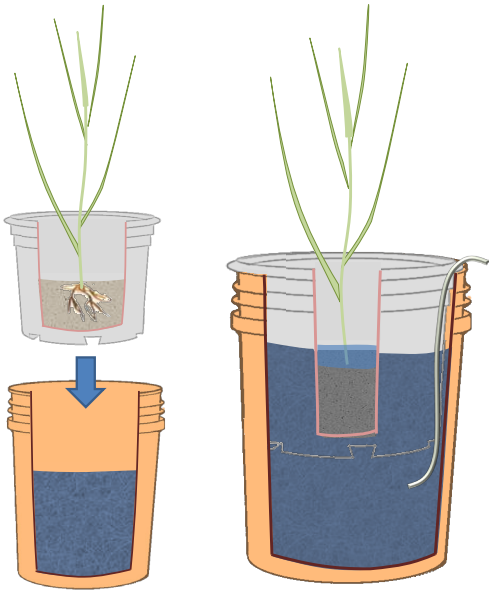
APPENDIX 2: SUPPLEMENTARY TABLES AND FIGURES



Appendix 2.1 Genetic variation among *Spartina alterniflora* genotypes over eight loci; Vermilion (V) and CP cultivars and genotypes from Catfish Lake, LA (CF), Bay Jimmy, LA (BJ), and Jamaica Bay, NY (NY) are distinguished by labels and marker color; each group is comprised of individuals sharing a "primary" genotype, designated "1"; four individuals possessed unique "secondary" genotypes, designated "2"; the primary CF genotype was identical to the V genotype, and is represented by the V marker

Appendix 2.2 Pairwise F_{ST} values between Bay Jimmy (BJ), Catfish Lake (CF-V), cultivar Vermilion (V), cultivar CP, and New York (NY) genotypes of *Spartina alterniflora*

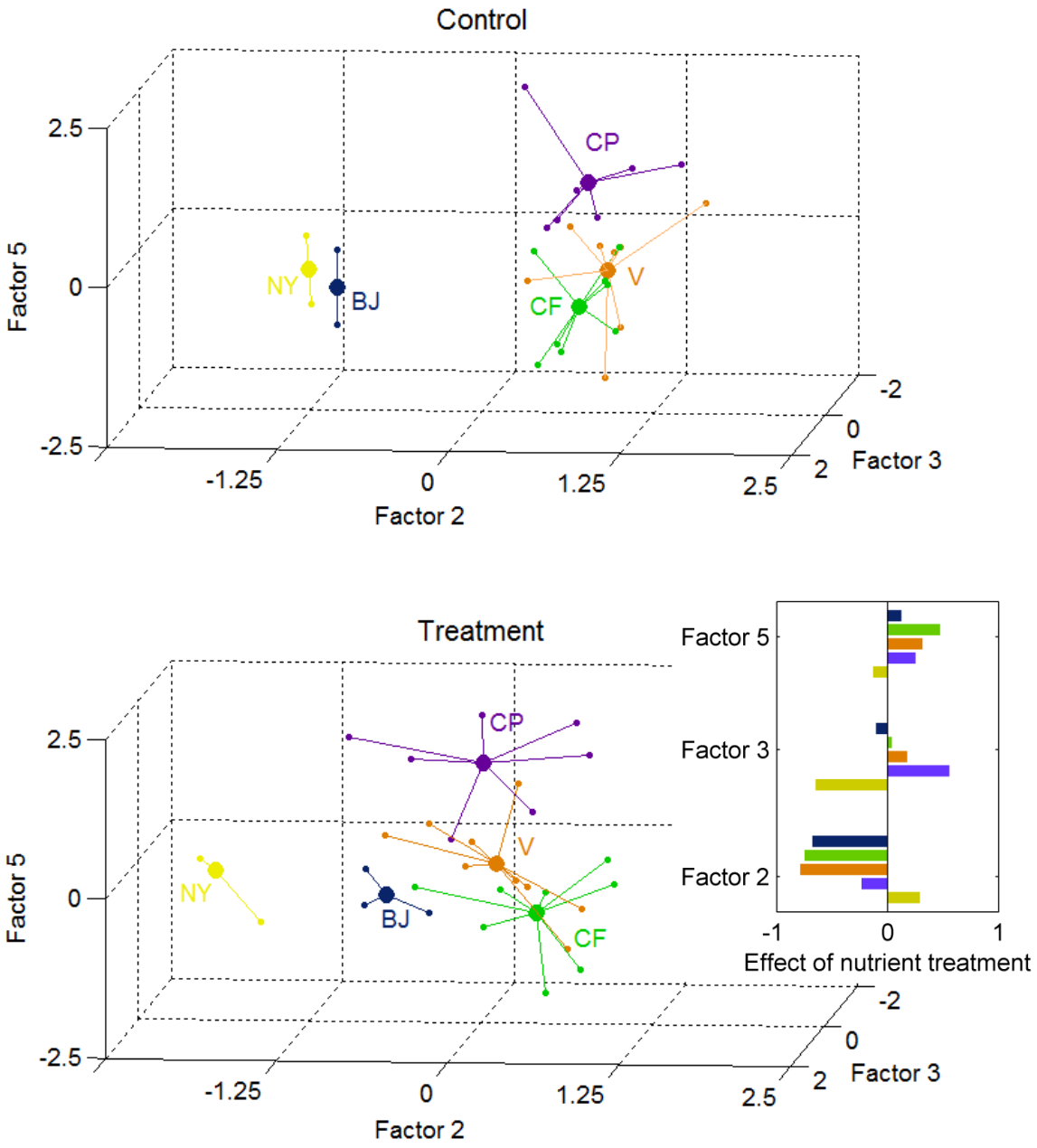
	BJ	CF-V	V	CP	NY
BJ	0.00				
CF-V	0.35	0.00			
V	0.36	0.22	0.00		
CP	0.27	0.34	0.44	0.00	
NY	0.49	0.59	0.62	0.45	0.00



Appendix 2.3 Experimental approach for simulating inflows and outflows

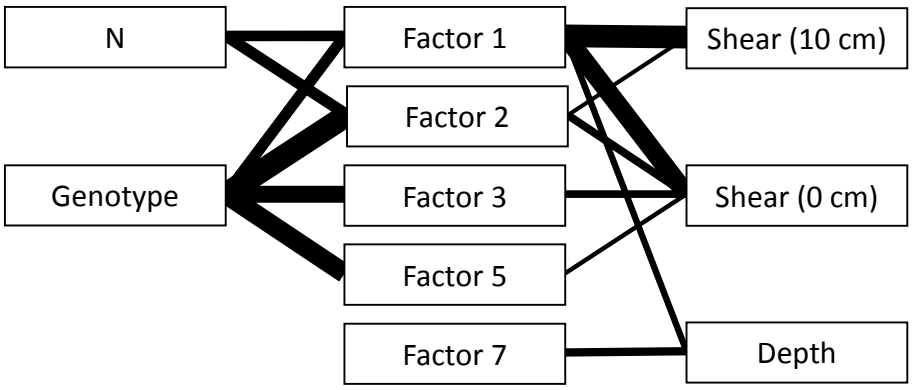
Appendix 2.4 Factors explaining overall *S. alterniflora* trait variation for loadings >0.60 (for factors that significantly differed among genotypes and/or nutrient treatments)

Factor (s^2 explained)	Trait	Loading
Factor 1 (33.7%)	BG biomass	0.99
	Rhiz.	0.94
	Root	0.93
	< 6 cm	0.93
	> 6 cm	0.91
	Root > 6 cm	0.89
	Rhiz. < 6 cm	0.89
	Rhiz. > 6 cm	0.78
	Root < 6 cm	0.77
	Biomass	0.91
	AG biomass	0.80
Factor 2 (16.0%)	N BG	-0.81
	CN BG	0.79
	Root:shoot	-0.78
	Shoot height	0.76
	Seed mass	0.71
	C AG	0.67
	No. seed heads	0.67
	Shoot diameter	0.66
Factor 3 (10.6%)	Root:rhiz.	0.98
	Root:rhiz. < 6 cm	0.86
	Root:rhiz. > 6 cm	0.73
Factor 4 (7.6%)	Intrinsic peak load	0.90
	Peak load	0.84
	Intrinsic UTS	0.84
Factor 5 (7.2%)	UTS	-0.84
	Rhiz. diameter	0.76
	No. leaves	0.74
Factor 6 (5.2%)	N AG	0.94
	CN AG	-0.92
Factor 8 (3.2%)	Leaf length	0.77



Appendix 2.5 Genotypic variation in multivariate components of tissue chemistry and plant growth traits for control and nutrient treatments. Eight multivariate factors explain 87.3% of the total variance across all traits (Supplementary Table 2); of the 5 factors that significantly differed among genotypes, factor 2 (x-axis), factor 3 (z-axis), and factor 5 (y-axis) captured the largest proportion of trait variation among genotypes based on

MANOVA η^2 values. Inset depicts changes in genotype centroid positions on each axis between treatments



Appendix 2.6 Relationships between nutrients, genotype, plant trait factors as described in Online Resource 4, and soil proxies of erosion resistance. Lines between variables indicate significant effects (running left to right), where line thickness represents the proportion of variation explained (R^2 and η^2). Note that this figure does not reflect a path analysis

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BIOGRAPHY

Brittany Marie Bernik moved to New Orleans to pursue her bachelor's degree in August 2005, three days before the city was devastated by Hurricane Katrina. In the aftermath of the storm, she dedicated herself to understanding coastal salt marshes, a disappearing habitat that provides storm surge protection as well as other critical ecosystem services. Originally from Richmond, Virginia, Brittany has lived longer in New Orleans, earning B.S. and M.S. degrees in Ecology & Evolutionary Biology from Tulane University, as well as a minor in Philosophy, before going on to complete her Ph.D. During the course of her undergraduate studies, Brittany worked with the entomology lab of Dr. L. Dyer studying the effect of storm disturbance on caterpillar-parasitoid dynamics, and was awarded an REU grant to continue researching tri-trophic interactions along an elevational gradient in Ecuador. She went on to work with the molecular ecology lab of Dr. M. Blum, examining the capacity of marsh species to evolve rapidly in response to environmental change, and earner her master's degree in 2010. In 2011 she was awarded a prestigious EPA STAR fellowship that allowed her to pursue Ph.D. research investigating how the extended phenotype of an engineer species influences salt marsh ecosystem function.