FEATURE ARTICLE

Soil erodibility differs according to heritable trait variation and nutrient-induced plasticity in the salt marsh engineer *Spartina alterniflora*

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ABSTRACT: Use of landform engineers for habitat restoration has often resulted in unanticipated outcomes. It is possible that departures from expectation arise because applications do not adequately account for the influence of heritable and non-heritable phenotypic variation on ecosystem attributes. In this study, we performed a common garden greenhouse experiment to determine whether soil shear strength—a characteristic linked to erosion resistance—varies according to heritable and plastic trait expression in *Spartina alterniflora* grown under contrasting nutrient regimes. We detected heritable variation across a broad spectrum of functional traits, including nutrient uptake. We also found that *S. alterniflora* exhibited trait-specific differences in nutrient-induced phenotypic plasticity. Heritable trait differences and plasticity together explained approximately 70% of the observed variation in soil shear strength. Soil shear strength increased when plants received more nutrients, but the influence of heritable variation on soil shear strength was equal to or larger than that of nutrient-induced plasticity. These findings illustrate that heritable and non-heritable trait expression can potentially govern the fate of marsh ecosystems, which suggests that consideration should be given to both factors when deploying landform engineers for coastal restoration.

KEY WORDS: Coastal eutrophication · Coastal protection · Ecosystem engineering · Ecosystem genetics · Erosion · Extended phenotype · Restoration · Salt marsh

For salt marshes dominated by grass species *Spartina alterniflora*, heritable and nutrient-induced trait variation strongly influence soil erodibility.

Photo: Brittany Bernik

INTRODUCTION

Though landform engineers are prized tools for habitat restoration, it is not uncommon for practical applications to result in unanticipated outcomes (e.g. Strong & Ayres 2013). Departures from expectation may arise because phenotypic variation is not taken into consideration, despite ample evidence that ecosystem attributes can be shaped by functional traits that exhibit heritable and non-heritable variation

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(Whitham et al. 2003, Corenblit et al. 2011, Eppinga et al. 2011, Pregitzer et al. 2013). Many engineering species are known to exhibit heritable variation in traits that exert influence on ecosystem attributes (i.e. a species' extended phenotype sensu Dawkins 1999). Engineers also typically exhibit phenotypic plasticity, where trait expression is subject to the influence of prevailing environmental conditions (Miner et al. 2005, Bardgett et al. 2014). Accordingly, understanding the influence of heritable and non-heritable trait expression on landform engineering could improve habitat restoration by better defining potential ecosystem outcomes.

Knowledge gained about the influence of heritable variation and phenotypic plasticity on landform engineering would be particularly valuable for salt marsh restoration. The landform engineer *Spartina alterniflora* (smooth cordgrass), which exhibits heritable and plastic trait expression (Seliskar et al. 2002, Travis & Grace 2010, Qing et al. 2012, Hughes 2014) is widely used for coastal marsh restoration because it can stabilize shorelines and increase surface elevation (Leonard & Luther 1995, Turner et al. 2002, Howes et al. 2010, Mudd et al. 2010). Despite some consternation about the introduction of non-native genotypes (Lesica & Allendorf 1999, Proffitt et al. 2005, Strong & Ayres 2013, Blum et al. 2014, Bernik et al. 2016), cultivars of *S. alterniflora* are nonetheless being incorporated into restorations with the aim of improving outcomes. For instance, the 'Vermilion' cultivar, which exhibits attributes that encourage establishment (LAPMC 1989, Fine & Thomassie 2000), is virtually the only stock used across the Louisiana coast (Utomo et al. 2010). It is possible, however, that use of cultivars does little to encourage landform engineering because cultivation for preferred traits can result in functional trade-offs. For example, phenotypes selected for greater aboveground growth may provide less soil stabilization because of reduced belowground investment (Herms & Mattson 1992). Novel outcomes may also arise because cultivars exhibit comparably narrow or distinct ranges of heritable trait variation, and because responses to prevailing environmental conditions may differ between cultivated and native genotypes.

In this study, we conducted a common garden greenhouse experiment to assess the influence of heritable variation and phenotypic plasticity on landform engineering by *S. alterniflora*. We compared phenotypic variation among genotypes drawn from wild and cultivated source populations under high and low NO_3^- treatments, focusing on tissue chemistry reflecting nutrient allocation, traits likely to influence erosion, as well as soil characteristics that are proxies of erosion resistance. This not only provided a first look at the relative influence of a species' extended phenotype and 'extended phenotypic plasticity' on geomorphology, it illustrated whether the use of cultivars is advantageous for marsh restoration. It also offered timely perspectives on ecosystem outcomes of nutrient loading, including whether diversion of nutrient-laden water from the Mississippi River stands to promote marsh creation or exacerbate coastal erosion in southeastern Louisiana.

MATERIALS AND METHODS

Source materials

We utilized material from 5 source populations that exhibit differences in both genetic identity and genetic diversity (see Table S1 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m601 p001_supp.pdf). To examine natural variation within a region, source material was collected from Bay Jimmy (LA1) and from a marsh ~40 km away in Catfish Lake (LA2). To examine a broader range of natural variation, source material was collected from a population near New York City (NY). At each site, plant material was harvested from a 5 × 5 m area. We also examined the cultivar 'Vermilion' (C1), which has been in wide use since 1989, as well as the more recently developed 'CP' cultivar (C2). Vermilion was developed for aboveground biomass production, transplantation survival, and tolerance to inundation and salinity (LAPMC 1989, Fine & Thomassie 2000), whereas CP was developed for high seed set and germination to enable aerial seeding (Utomo et al. 2010, Knott et al. 2012, 2013). We obtained starting stocks of C1 and C2 from nurseries at Nicholls State University, Thibodaux, LA, and the LSU AgCenter, Baton Rouge, LA, respectively. Both C1 and C2 were propagated from a single genotypic line.

Experimental design

Donor material from all 5 sources was vegetatively propagated, then grown under common garden greenhouse conditions for approximately 1 yr to create stocks for a full factorial common garden greenhouse experiment. Initiated in April 2013, the experiment spanned a full growing season. For each of the 10 treatment combinations (5 source populations × 2 NO_3^- conditions), 2 plants were randomly

established in each of 5 replicate blocks. Thus the experiment encompassed 100 plants total (5 provenances × 2 NO_3^- conditions × 5 replicates × 2 subsamples = 100 plants). Individuals were established using whole-plant single-stems cut to 5 cm, constituting a reduction to 3–7 g starting material. Potting material included soil collected from a salt marsh in the Pointe-aux-Chênes Wildlife Management Area (Louisiana), which was 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 of Scotts Osmocote Plus, a patterned-release complete nutrient fertilizer containing 15% N, 9% P, and 12% K, to supply all plants with an adequate base level of resources for the duration of the experiment, releasing at maximum 1 g m^{-2} per month NO_3^-. Pots were placed inside buckets containing 13 l of water treated with Instant Ocean® Sea Salt (Blacksburg, VA) to attain 5 ppt salinity, with water levels held approximately 3 to 4 cm above the soil surface after the first week of the experiment (Fig. S2 in the Supplement). To minimize salt accumulation above the soil surface, salt additions were omitted from inflows every other week, keeping concentrations to an average of 5 ppt. 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® $NaNO_3$ pot^{-1}, bringing NO_3^- concentrations up to 10 mg l^{-1}. While NO_3^- concentrations for the lower Mississippi River are only 1 to 3 mg l^{-1} on average, marshes fed by river diversions are expected to receive a median estimate of 60 g m^{-2} per year NO_3^- 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 m^{-2} yr^{-1} (Mitsch et al. 2005).

Genetic characterization

Adapting methods from Blum et al. (2007), we assessed allelic variation across a panel of 8 microsatellite markers to characterize genetic diversity and differentiation among plants from different source populations. Except for C1, which exhibited 1 genotype for all 20 individuals, plants from each source population exhibited 2 genotypes: 1 unique to a single individual, and another shared by the remaining 19 individuals. A principal coordinates analysis (PCoA) of allelic variation recovered distinct clusters of genotypes from LA1, LA2, NY, and C2 populations (Fig. S1). However, some LA2 plants exhibited a genotype that was indistinguishable from C1 (Fig. S1), which indicates that LA2 plants were either Vermilion cultivars introduced to Catfish Lake, or that cultivar alleles have introgressed into nearby natural populations as a result of admixture. Accordingly, we proceeded with the expectation that little if any performance difference would be found between LA2 and C1 plants. Log-likelihood calculations assigned genotypes to the correct source with 100% accuracy, and pairwise Ritland and Lynch relatedness metrics (RLM) provide further evidence of dissimilarity between groups, revealing relatedness between individuals from the same provenance but not among provenances, allowing for the shared genotype between C1 and LA2 (Lynch & Ritland 1999) (Table S1).

Phenotypic trait and soil analysis

Plant traits and soil characteristics were measured after Week 28 of the experiment. At that time, all aboveground (AG) and belowground (BG) biomass 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 (with 'shoot' referring to AG material, not inclusive of BG rhizomes). Shoot height, shoot diameter, seed head length, the number of living leaves per shoot, and the length of live leaves were measured for 3 mature shoots (or 3 shoots representing the canopy vegetation, if seed heads were not present) for average measures per pot. The total weight of seed heads was also 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 Systems) was then used to measure the force necessary to induce failure (peak load) and to calculate the ultimate tensile strength (UTS, i.e. force per area) of rhizomes. The cross-sectional area of each rhizome segment was also recorded. Each biomass component was then oven-dried to obtain constant mass weights and to calculate AG and BG biomass, and ratios of AG to BG biomass (shoot:root ratio) as well as root to rhizome biomass (root:rhizome ratio) and upper to lower soil horizon biomass (BG depth ratio). Immediately after harvesting AG biomass (and prior to harvesting BG biomass), torque measurements were taken using a shear vane (Seiken) at 2 points

just below the soil surface (0 cm) and within the lower soil horizon (10 cm). These measurements were used to calculate soil shear strength, which is a proxy of erosion resistance (Amer et al. 2017). Average soil depth was calculated from measures taken at the center and perimeter edge of each pot prior to harvesting BG biomass.

Nutrient uptake analysis

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 h after, and 1 wk after the final inflow replacement to determine NO_2^- and NO_3^- concentrations. After Week 28, the volume of outflow was also measured in order to calculate the mass abundance of retained nutrients. Additionally, standardized dry leaf and rhizome samples from each pot were ground and homogenized using a mortar and pestle. Homogenized samples were analyzed using an EA112 Element Analyzer (Thermo Scientific) to measure total C and N concentrations.

Statistical analyses

For all variables other than nutrient removal, the effects of source population (hereafter referred to as 'provenance') and nutrient treatment were tested using factorial ANOVAs (Table S2). To account for 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 (test statistic K) were used to evaluate the effect of provenance within controls and within treatments, and to test for a nutrient effect over all samples without including provenance 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 provenance using Fisher's least significant difference (LSD) and Dunn's tests. Differences in nutrient removal over time were compared using repeated-measure ANOVAs.

A factor analysis was also 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). Following Hester et al. (2001), significant factors were included in a 2-way MANOVA (see Table 1) to test for differences according to provenance and nutrient treatment. Stepwise linear regression was then conducted to determine which factors explained the largest proportion of variation in each soil characteristic. Stepwise linear regression was also used to assess the effects of BG biomass and architecture, including roots versus rhizomes, on soil shear strength.

RESULTS

Phenotypic trait variation

All measured traits exhibited heritable variation (Figs. 1 & 2), where plants of different provenance exhibited a distinct combination of trait differences. At the end of the experiment, the number of surviving plants (*N*) in control and nutrient treatments were: $N_{LA1} = 2, 4$; $N_{LA2} = 9, 8$; $N_{C1} = 9, 10$; $N_{C2} = 8, 9$; and $N_{NY} = 2, 8$, respectively. LA1 exhibited the highest mortality rates, low fecundity, and low biomass—particularly AG biomass—despite exhibiting the longest leaves (Fig. 1; some data not shown). LA1 plants distinctively invested more towards roots than rhizomes, and exhibited the greatest average proportion of BG biomass distributed in the shallower soil horizon (Fig. 1). LA2 plants exhibited intermediate expression of most traits, including those associated with productivity and fecundity. However, LA2 plants had tall shoots, the highest mean UTS, and the highest intrinsic UTS. C1 plants consistently expressed some of the highest average biomass measures and experienced the lowest level of mortality. In addition to tall shoots, C1 plants produced the largest number of seed heads, and exhibited intermediate mean and intrinsic UTS values. C2 plants exhibited trait tradeoffs, with the thickest shoots but the lowest shoot density, and produced large numbers of seeds but few seed heads. As shoot and rhizome thickness tended to correlate (Figs. 1 & 2), C2 also had the thickest rhizomes on average as well as the lowest UTS and highest peak load values. NY plants also exhibited tradeoffs, showing the highest shoot density but the thinnest shoots and rhizomes, with the lowest average peak load values. NY plants also exhibited the lowest mean and intrinsic UTS values.
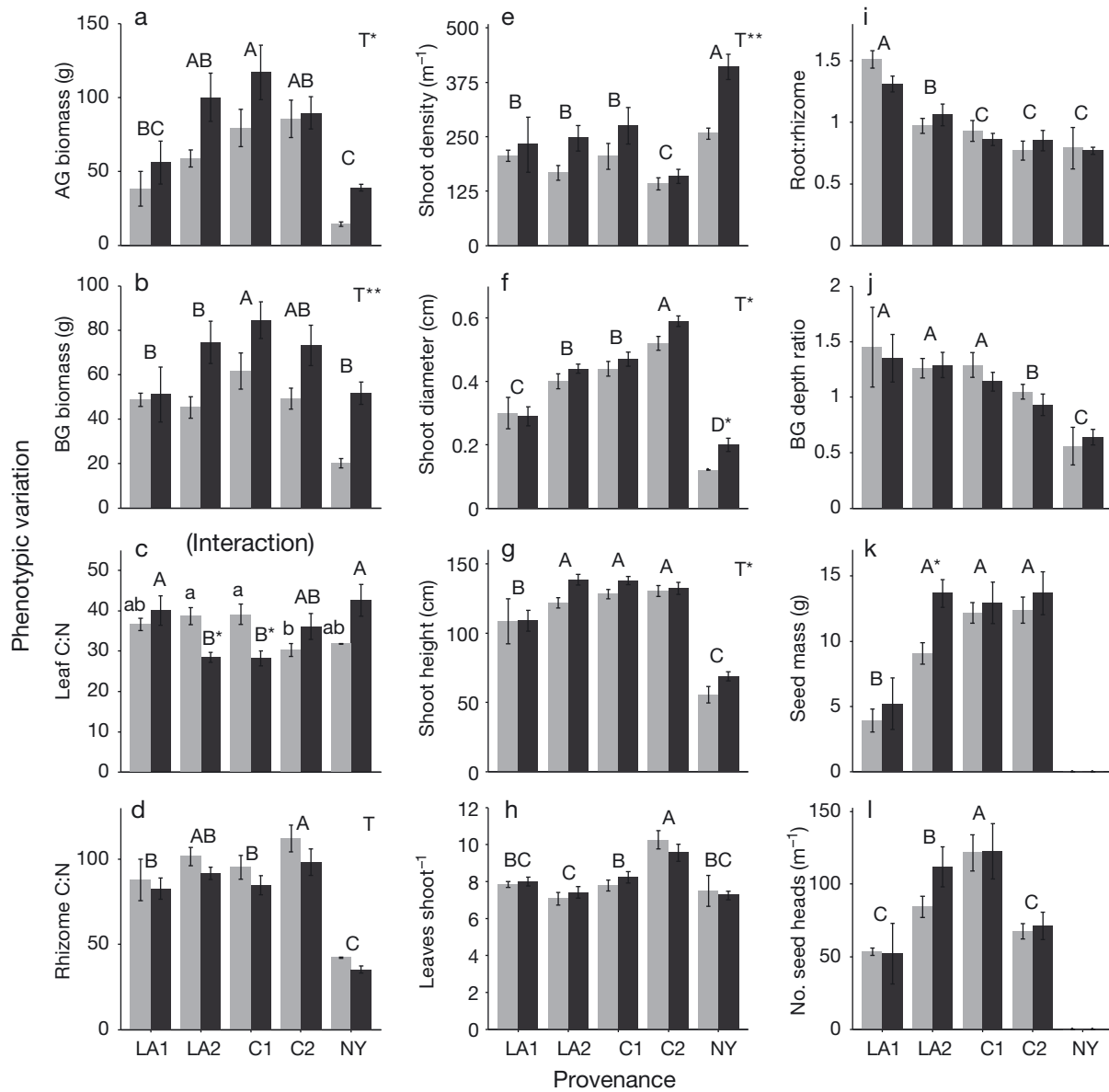
Fig. 1. Phenotypic variation (mean ± SE) among *Spartina alterniflora* from Bay Jimmy, LA (LA1), Catfish Lake, LA (LA2), and Jamaica Bay, NY (NY), as well as in the Vermilion (C1) and CP (C2) cultivars under control conditions (light gray) and elevated NO_3^- treatments (dark gray). AG = aboveground, BG = belowground. See Table S2 in the Supplement for detailed ANOVA results. At the top right of panels, T indicates a nutrient approaches (p < 0.10), or achieves significance (T* p < 0.05, T** p < 0.01), and no T indicates no nutrient effect (p ≥ 0.10). In (c), significant provenance × nutrient effects are labelled 'Interaction' in parentheses. When non-parametric tests were neccessary, separate tests evaluated the effect of provenance within controls (lower-case letters) and treatments (upper-case letters), as well as the effect of nutrients without provenance as a factor. Above bars, * indicates a significant nutrient effect and different letters indicate significant pairwise differences

In addition, NY plants exhibited the shortest average shoot height, the lowest biomass measures, and they did not produce seed heads.

Eight multivariate factors cumulatively explained 87.3% of the total variance across all traits (Table 1). The first factor, which corresponded to AG and BG biomass, explained the largest proportion of total variance (33.7%) and significantly differed by prove-nance ($F_4 = 2.84$, p = 0.03, $_p\eta^2 = 0.17$, where $_p\eta^2$ is the partial effect size). Five other factors that explained an additional 44.6% of the total variance also significantly differed by provenance: factor 2 ($F_4 = 40.93$, p < 0.001, $_p\eta^2 = 0.75$), factor 3 ($F_4 = 9.37$, p < 0.001, $_p\eta^2 = 0.41$), factor 4 ($F_4 = 5.82$, p = 0.001, $_p\eta^2 = 0.30$), factor 5 ($F_4 = 15.47$, p < 0.001, $_p\eta^2 = 0.53$); and factor 8 ($F_4 = 4.54$, p = 0.003; $_p\eta^2 = 0.25$%; Table 1; Fig. S3 in
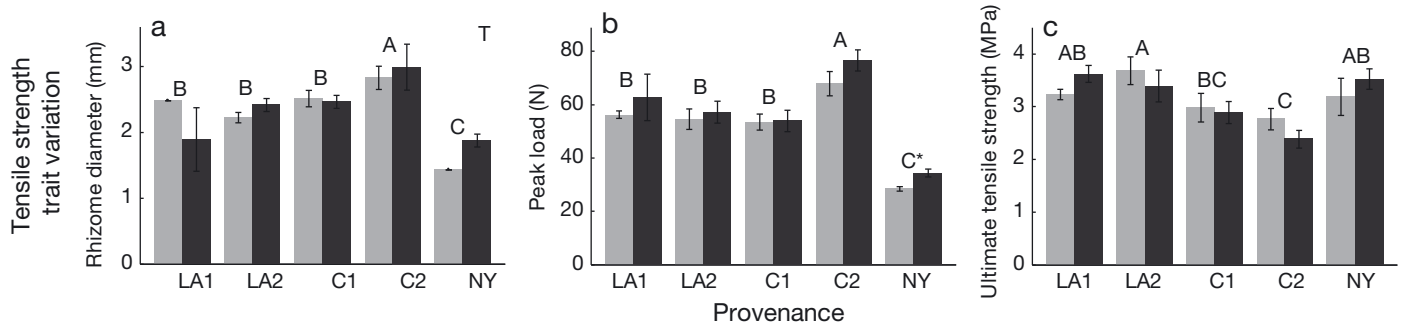
Fig. 2. Differences in tensile strength traits (mean ± SE) among *Spartina alterniflora* from Bay Jimmy, LA (LA1), Catfish Lake, LA (LA2), and Jamaica Bay, NY (NY), as well as in the Vermilion (C1) and CP (C2) cultivars under control conditions (light gray) and elevated NO_3^- treatments (dark gray). See Table S2 for detailed ANOVA results. At the top right of (a), T indicates a nutrient effect that approaches but does not achieve significance (p < 0.10). Above bars, • indicates a significant nutrient effect and different letters indicate significant pairwise differences

Table 1. Factors (F1–F8) explaining *Spartina alterniflora* trait variation, and their response to experimental treatments. Traits with >0.60 loading (L) are listed and parentheses give proportion variation explained (s^2). Bold indicates significance (α = 0.05). Abbreviations and acronyms refer to: above- (AG) and belowground (BG), BG rhizome (rhizome), carbon and nitrogen mass or ratio (e.g. C:N ratio), number (no.), intrinsic (int., i.e. controlling for area), and ultimate tensile strength (UTS)

| Factor (s^2)	——— Trait loading ——— Factor traits	L	Provenance (P) $F_{4,50}$	p	$_p\eta^2$	— Nutrient (N) — $F_{1,50}$	p	$_p\eta^2$	—— P × N —— $F_{4,50}$	p	$_p\eta^2$	——— Block ——— $F_{4,50}$	p	$_p\eta^2$
F1 (0.34)	BG biomass	0.99	2.61	**0.047**	0.17	10.96	**0.002**	0.18	0.55	0.70	0.04	4.15	**0.01**	0.25
	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												
F2 (0.16)	N BG	−0.81	43.33	**<0.001**	0.78	11.44	**0.001**	0.19	2.00	0.11	0.14	1.56	0.20	0.11
	C:N BG	0.79												
	BG:AG	−0.78												
	Shoot height	0.76												
	Seed mass	0.71												
	C AG	0.67												
	No. seed heads	0.67												
	Shoot diameter	0.66												
F3 (0.11)	Root:rhizome	0.98	17.10	**<0.001**	0.58	0.01	0.93	0.00	1.03	0.40	0.08	9.59	**<0.001**	0.43
	<6 cm	0.86												
	>6 cm	0.73												
F4 (0.08)	Int. peak load	0.90	5.36	**0.001**	0.30	1.22	0.28	0.02	0.37	0.83	0.03	1.53	0.21	0.11
	Peak load	0.84												
	Int. UTS	0.84												
F5 (0.07)	UTS	−0.84	16.97	**<0.001**	0.58	1.64	0.21	0.03	0.60	0.66	0.05	2.21	0.08	0.15
	Rhiz. diameter	0.76												
	Leaves shoot^{-1}	0.74												
F6 (0.05)	N AG	0.94	0.61	0.66	0.05	0.21	0.65	0.00	5.53	**0.001**	0.31	1.53	0.21	0.11
	C:N AG	−0.92												
F7 (0.04)	Outflow salinity	0.87	1.38	0.26	0.10	9.48	**0.003**	0.16	0.40	0.81	0.03	26.41	**<0.001**	0.68
	Outflow volume	−0.71												
F8 (0.03)	Leaf length	0.77	4.97	**0.002**	0.28	3.13	0.08	0.06	0.62	0.65	0.05	3.26	**0.02**	0.21
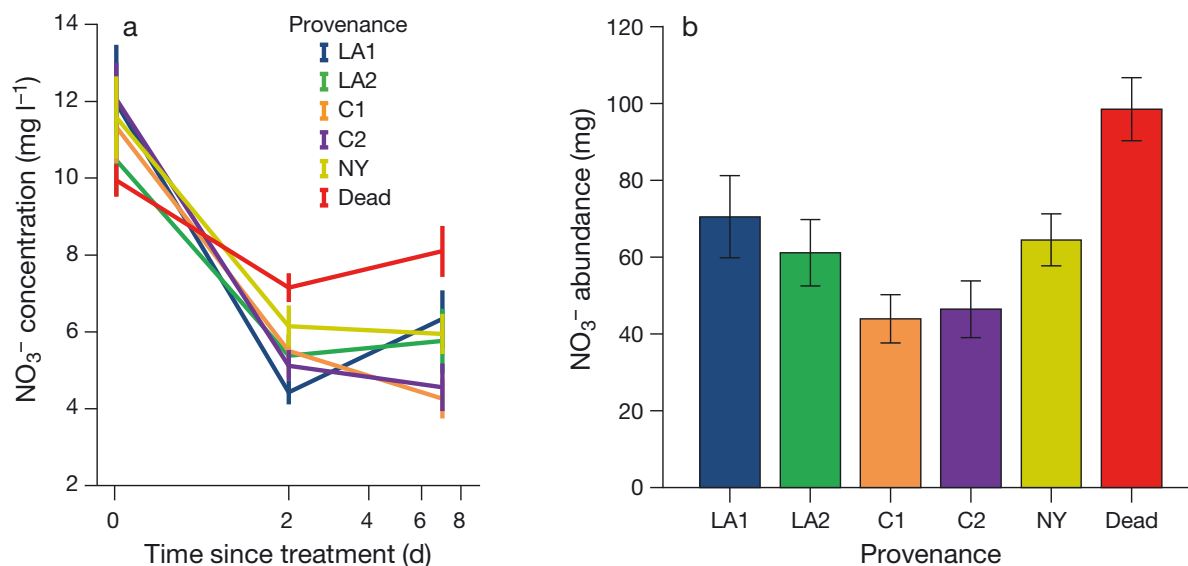
Fig. 3. Differences (mean ± SE) among *Spartina alterniflora* from Bay Jimmy, LA (LA1), Catfish Lake, LA (LA2), and Jamaica Bay, NY (NY), as well as in the Vermilion (C1) and CP (C2) cultivars following nutrient addition in (a) groundwater NO_3^- concentrations over time and (b) final groundwater NO_3^- abundance

the Supplement). Based on MANOVA $_p\eta^2$ values (Table 1), the 3 factors that captured the largest proportion of trait variation according to provenance were factor 2 (corresponding to C:N, shoot diameter, shoot height, shoot:root ratio, and fecundity), factor 3 (corresponding to root:rhizome ratio), and factor 5 (corresponding to UTS, rhizome diameter and number of leaves; Table 1). These 3 factors explained 16, 10.6, and 7.2% of the total trait variance, respectively. Provenance explained 75.2, 40.7, and 52.7% of the variance in each factor.

Fewer traits differed according to nutrient conditions. The effect of nutrient treatment on traits was also typically similar to or smaller than provenance (Figs. 2 & 3), and the proportion of variance explained by nutrients was relatively low. Of the 8 factors characterizing the majority of overall trait variation, only 3 differed between control and elevated nutrient treatments: factor 1, factor 2, and factor 7; Table 1, Figs. 1 & S3. As described by factor 1, elevated nutrients had a positive effect on AG and BG biomass (from 0–6 cm and >6 cm depths; Fig. 1). As described by factor 2, shoot thickness, height, and inflorescence length were all significantly higher under elevated nutrient conditions (Fig. 1). Shoot density (which did not load strongly with any factor) was also significantly higher under elevated nutrient conditions (Fig. 1).

Factorial ANOVAs (Table S2) offered little power (<0.20) to detect heritable differences in trait responses to nutrients, but post hoc comparisons of

pairwise differences among source populations between control and elevated nutrient treatments offered some evidence of interactions (Figs. 2 & 3). For traits other than shoot density, the magnitude rather than the direction of the response to nutrients differed by provenance (Figs. 2 & 3). For example, elevated nutrient conditions increased AG and BG (i.e. overall) biomass, but had no effect on the ratio of AG to BG biomass (i.e. shoot:root ratio) (Table S2). Similarly, it had no effect on AG productivity in C2 plants, or on BG productivity in LA1 plants (Fig. 1). Additionally, LA2 (but not C1) plants exhibited a 33% increase in seed heads and a 51% increase in seed mass (Fig. 1) under elevated nutrient conditions.

Nutrient uptake

Tissue chemistry differed according to provenance as well as nutrient availability. NY plant tissue exhibited a significantly lower rhizome C:N ratio, having 88% higher BG N concentrations on average compared to all other source populations. As described by factor 2, rhizome N concentration and C:N were also significantly higher under elevated nutrient conditions (Fig. 1). We also detected interactions between provenance and nutrient availability. The most apparent interaction occurred with leaf C:N. This response was also evidenced by a significant interaction between provenance and treatment for

factor 6 (F_4 = 5.01, p = 0.002). Notably, LA2 and C1 plants also exhibited increased leaf N concentrations, while other plants exhibited a decrease—particularly NY plants (which instead exhibited higher rhizome N concentrations).

Differences were also detected in nutrient uptake. Although LA1 plants attained the highest mean NO_3^- concentration after exhibiting a large initial decline (Fig. 3), changes in NO_3^- concentrations over time did not differ according to provenance (F_4 = 1.18, p = 0.34). However, differences in NO_3^- by mass were informative when accounting for variation in water loss (K_4 = 9.08, p = 0.06). Post hoc tests indicated that NO_3^- was significantly higher for LA1 and NY plants than C1 plants (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 in NO_3^- were found between LA2 and C2 plants. Examination of changes in NO_2^- revealed no additional N trends according to provenance (F_4 = 0.40, p = 0.81).

Soil characteristics

Soil elevation did not differ according to provenance ($F_{4,55}$ = 0.99, p = 1.23; Fig. 4), but it significantly increased under high nutrient conditions ($F_{1,55}$ = 5.31, p = 0.03, $_p\eta^2$ = 0.09), by 2% on average. Stepwise regression showed that factor 7 (salinity and water outflow volume) explained 31% of observed variation (Fig. 4, Fig. S4 in the Supplement), and factor 1 (biomass) explained an additional 24% of observed variation ($F_{2,61}$ = 5.40, p = 0.01, R^2 = 0.12; Figs. 4 & S4).

Shallow soil shear strength differed according to provenance and was best explained by differences in biomass (Table 1, Figs. 4 & S4). At the soil surface, shear strength significantly differed according to provenance ($F_{4,55}$ = 7.52, p < 0.001, $_p\eta^2$ = 0.35) and nutrient treatment ($F_{1,55}$ = 4.53, p = 0.04, $_p\eta^2$ = 0.08). Compared to the average, soil shear strength was 43% lower with NY plants and 37% higher with C1 plants (but only 9% higher with LA2 plants). Stepwise 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. 4). Factor 1, corresponding to biomass, had the strongest effect size (β = 0.71; Fig. S4). Breaking down components of factor 1 using stepwise regression and semipartial correlations revealed that BG biomass explained 52.5% of the variation in surface shear strength, with another 3.1% uniquely explained by AG biomass
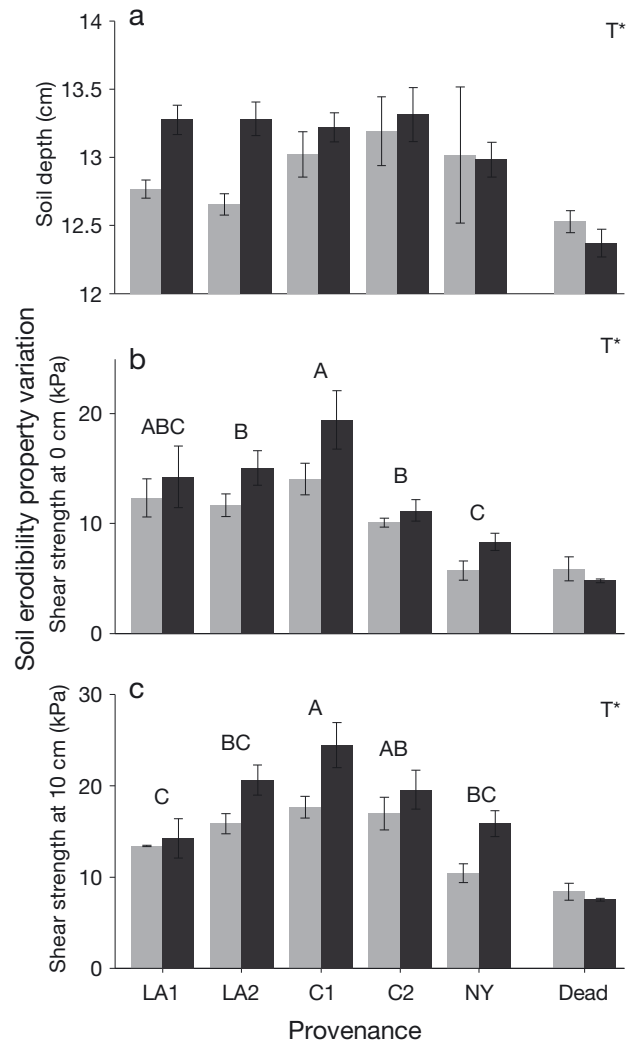

Fig. 4. Differences (mean ± SE) in proxy measures of erosion-buffering engineering activities among *Spartina alterniflora* from Bay Jimmy, LA (LA1), Catfish Lake, LA (LA2), and Jamaica Bay, NY (NY), as well as in the Vermilion (C1) and CP (C2) cultivars under control (light gray) and elevated NO_3^- treatments (dark gray). See Table S2 for detailed ANOVA results. At the top right of each panel, T* indicates a treatment effect (p < 0.05). Above bars, different letters indicate significant pairwise differences

($F_{2,65}$ = 41.87, p < 0.001). Of variation explained by BG biomass, 54.7% was uniquely explained by shallow roots and 13.6% by deep rhizomes (while the other components did not significantly improve the model; $F_{4,67}$ = 38.42, p < 0.001).

Shear strength at the deeper soil horizon also significantly differed by provenance ($F_{4,55}$ = 4.24, p = 0.01, $_p\eta^2$ = 0.24) and among nutrient treatments ($F_{1,55}$ = 8.00, p = 0.01, $_p\eta^2$ = 0.13; Fig. 4). Over control and nutrient treatments, C1 plants elevated shear strength (10 cm) by 25% above average, while LA1

and NY plants reduced it by 18 and 22% below average, respectively. Shear strength (10 cm) was 28% higher on average in elevated nutrient treatments. The stepwise regression model for shear strength (10 cm) indicated that factors 1 and 2 explained 73.1% of the observed variation ($F_{2,63}$ = 86.71, p < 0.001), with factor 1 having the largest effect size (β = 0.85; Fig. S4). Repeating the analysis for factor 1 traits revealed that BG biomass components explained 72.0% of the variation in shear strength (10 cm), with another 4.6% uniquely explained by AG biomass ($F_{2,65}$ = 109.59, p < 0.001). Of variation explained by BG biomass, 19.9% was uniquely explained by shallow roots, 18.0% by deep rhizomes, 15.5% by shallow rhizomes, and 12.1% by deep roots ($F_{4,63}$ = 43.14, p < 0.001).

DISCUSSION

Practical applications of landform engineers often do not consider whether outcomes are attributable to heritable or non-heritable phenotypic variation. Our common garden greenhouse experiment showed that differences in plant attributes and soil characteristics associated with erosion resistance correspond to heritable and non-heritable variation in the salt marsh engineer *Spartina alterniflora*. A suite of phenotypic traits, including traits likely to mediate erosion resistance, exhibited both heritable variation and plasticity in response to nutrients. Notably, cultivars exhibited considerable phenotypic plasticity, comparable to levels expressed by plants drawn from natural populations. We found that soil shear strength increased when plants received more nutrients; however, we also found that provenance had an equal or larger influence than nutrient-induced plasticity on soil shear strength. These findings illustrate that heritable and non-heritable trait variation can potentially govern the fate of marsh ecosystems, which suggests that consideration should be given to both factors when deploying landform engineers like *S. alterniflora* for coastal restoration.

Heritable variation and phenotypic plasticity in *Spartina alterniflora*

Cultivars and plants drawn from natural sources differed across all measured traits under common garden conditions, indicating that *S. alterniflora* exhibits considerable heritable phenotypic variation, and thus affirming prior findings (Seliskar et al. 2002,

Proffitt et al. 2005, Travis & Grace 2010, Hughes 2014). Phenotypic variation in *S. alterniflora* has been interpreted as evidence of adaptation to stressor exposure resulting in morphological specialization (Hester et al. 1998, Smith & Proffitt 1999, Proffitt et al. 2003). Consistent with this, we found that NY plants exhibited low biomass and seed production, which may reflect demands for resource conservation under comparably shorter growing seasons at northern latitudes. We also found that the CP (C2) cultivar, which has been selected for increased fecundity, produced heavier seed heads, though other plants produced more seeds. Other evidence suggests, however, that some *S. alterniflora* are generalists capable of performing well across a range of environmental conditions (Proffitt et al. 2003). The Vermilion (C1) cultivar, for example, attained high biomass, low levels of mortality and relatively high fecundity under contrasting nutrient conditions.

Like prior studies, we found that *S. alterniflora* exhibits heritable variation in nutrient uptake. Differences in sensitivity to nutrient availability have been observed among *S. alterniflora* drawn from distinct source populations, including variation in N uptake, allocation, and use efficiency (Qing et al. 2012). Intraspecific variation in salt stress resistance, which can influence nutrient uptake, has also been observed among *S. alterniflora* populations (Hester et al. 2001). Under high salinity conditions, *S. alterniflora* must invest nitrogen in glycine betaine synthesis to maintain the osmotic balance needed for water uptake and transport (Cavalieri & Huang 1981). Individuals with a limited ability to exclude or secrete salt ions also tend to invest more heavily in belowground growth (Hester et al. 2001), which is consistent with the lower shoot:root and rhizome N concentrations observed in NY plants. Variation in the ability to synthesize osmoregulatory compounds may also explain the reduced water loss and increased nutrient outflow we observed in LA1 plants (Bradley & Morris 1991, Hester et al. 2001). Further study is warranted to determine the physiological basis of heritable variation in nutrient uptake, however, as it could also reflect osmoregulation and associated conditions like oxygen availability and sulfide concentrations (Morris 1980).

As expected, we detected evidence of phenotypic plasticity—for example, elevated nutrients promoted greater biomass and increased shoot diameter, height, and density—but we also found that plasticity differed according to provenance, which suggests that *S. alterniflora* exhibits heritable variation in phenotypic plasticity. It is well understood that AG and BG

attributes vary in response to resource availability and stressor exposure (Mendelssohn & Morris 2000, Bertness et al. 2008, Darby & Turner 2008a,b, Morris et al. 2013a,b, Zhang et al. 2013, Liu et al. 2016). Phenotypic plasticity can be advantageous for plants like *S. alterniflora* that undergo vegetative reproduction, as it can enable clones to persist over shifting environmental conditions—particularly in extreme environments like coastal salt marshes that experience salinity and inundation stress (Douhovnikoff & Dodd 2015). Heritable variation in plasticity can also be advantageous, since the demand and value of plasticity can depend on the nature of prevailing environmental conditions (Sultan 2000). Our findings are consistent with this expectation, where trait-specific differences in response to N enhancement appear to correspond to variation in resource allocation strategies. For instance, exposure to elevated nutrients resulted in higher seed production in LA2 plants, whereas it resulted in greater shoot diameter and density in NY plants. Such differences suggest that resource investments necessary to cope with environmental variation along the northern Gulf coast differ from those necessary to cope with conditions across the mid-Atlantic coast (Seliskar et al. 2002). Additional comparisons, especially among more genotypes drawn from within the same region, would better illustrate whether differences in plasticity reflect alternative responses to common stressors or specialization to local conditions.

Though our findings indicate that plasticity is heritable, it is also possible that the observed variation is a consequence of epigenetic regulation of trait expression. As has been found in *S. alterniflora* and other species (Verhoeven et al. 2010, Bräutigam et al. 2013, Kilvitis et al. 2014, Verhoeven & Preite 2014, Douhovnikoff & Dodd 2015, Foust et al. 2016), epigenetic regulation may allow clones to respond to changing environmental conditions. This would help explain the observed differences in responses to nutrients between LA2 and Vermilion plants, which appear to exhibit the same genotype (Fig. S1). Alternatively, trait expression may differ between individuals with the same apparent genotype due to differences in genetic mutation loads accumulated over the course of clonal propagation (Klekowski 1997). 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 inform restoration practices that are based on expectations of predictable and consistent expression of cultivated traits.

The extended phenotype of a landform engineer

We found further evidence that *S. alterniflora* exhibits an extended phenotype that influences ecosystem attributes (Seliskar et al. 2002, Proffitt et al. 2005, Violle et al. 2007, Nie et al. 2010, Travis & Grace 2010, Hughes 2014). Like prior studies showing that *S. alterniflora* exhibits heritable variation in phenotypic 'effect' traits (Seliskar et al. 2002, Proffitt et al. 2005, Violle et al. 2007, Travis & Grace 2010, Cornelissen et al. 2014, Hughes 2014), we found that *S. alterniflora* exhibits heritable variation in traits that can influence ecosystem attributes. For example, heritable variation in architecture (e.g. stem density) can influence sediment deposition and accretion (Leonard & Luther 1995). Similarly, variation in biomass can translate to differences in productivity that influence marsh surface elevation (Turner et al. 2002).

We also found clear evidence that the extended phenotype of *S. alterniflora* encompasses landform engineering. Surface and sub-subsurface soil shear strength, which serves as a proxy measure of erosion resistance, differed according to plant provenance. The effect sizes we observed were similar to those that have been found in other studies showing community and ecosystem outcomes of heritable variation in *S. alterniflora* (Seliskar et al. 2002, Proffitt et al. 2003, Travis & Grace 2010). While the potential for engineering species to modify landform dynamics is becoming increasingly recognized (Corenblit et al. 2011), this study is the first to illustrate that geomorphology is mediated by intraspecific variation in a landform engineer. This finding is not entirely surprising, however, considering that prior studies have shown that heritable variation in *S. alterniflora* can influence associated ecosystem attributes like the quantity and distribution of soil organic matter and microbial activity (Seliskar et al. 2002, Proffitt et al. 2005, Nie et al. 2010). It also builds on observations that plant species vary in capacity to influence Earth surface processes and suggestions that adaptive variation in plants can shape biogeomorphic feedbacks (Corenblit et al. 2011).

After accounting for measures of productivity, the factors that best explained variation in shear strength corresponded to the traits that distinguished plants from different source populations. This is consistent with evidence from a field-scale common garden experiment (Bernik 2015) indicating that differences in shoreline erosion rates are likely due to variation in traits other than BG biomass production. We found corroborative evidence of a more subtle mechanism

of soil modification, whereby the effect of BG biomass on shear strength is mediated by relative allocations to fine root production versus rhizomes, with greater fine root production accounting for a higher proportion of the observed variation in shear strength.

Soil shear strength measures may not fully capture the contributions of root tensile strength (i.e. UTS) to erosion resistance. The overall shear strength for a section of a root mat likely corresponds to the product of UTS and the total cross sectional area of roots and rhizomes that must break for shearing to commence (van Eerdt 1985, Tengbeh 1993, Howes et al. 2010). Our findings illustrate that *S. alterniflora* exhibits the inverse power relationship between root (i.e. rhizome) diameter and tensile strength that has been observed in other systems (van Eerdt 1985, Gyssels et al. 2005, De Baets et al. 2008). We also found that both rhizome diameter and tensile strength varied according to provenance, and that they do not necessarily increase erosion resistance. For example, C2 plants had thick rhizomes that could withstand the highest force (i.e. peak load), but exhibited the lowest UTS. Plants 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 those of other plants examined here (Fig. 2). Low UTS and weaker rhizomes were also observed for the Vermilion (C1) cultivar, which notably contrasts with the high UTS values exhibited by LA2 plants (Fig. 2). It remains possible that these and other traits (e.g. shoot diameter and density, root diameter, fine roots) influence erosion resistance by modifying other soil attributes (i.e. besides elevation and shear strength) that are better characterized through field-scale experiments (Bouma et al. 2005, Leonard & Croft 2006, Yang et al. 2008, Burylo et al. 2012, Fagherazzi et al. 2012, 2013).

Extended phenotypic plasticity in a landform engineer

Though prior work on heritable variation involving reciprocal transplants suggested that ecosystem-level effects of phenotypic plasticity (i.e. extended phenotypic plasticity) are minor (Seliskar et al. 2002), nutrient addition resulted in increased surface elevation and it led to responses that increased measures of erosion resistance, regardless of provenance. An experiment examining the extended phenotype of *Phalaris arundinacea* similarly detected evidence of heritable variation in plasticity, but found that nutrient availability controlled the competitive advantage

of specialist genotypes by stimulating or suppressing differences in engineer traits (Eppinga & Molofsky 2013). In contrast, we also found that differences in the extended phenotype of *S. alterniflora* persisted regardless of nutrient regime.

The observed range of extended phenotypic plasticity was nonetheless smaller relative to the range of heritable phenotypic differences found among *S. alterniflora* from different source populations (Seliskar et al. 2002). This finding provides an intriguing counterexample to the well-documented and often-cited extended phenotype of *Populus tremuloides* (Whitham et al. 2006). Effects of *P. tremuloides* genotypes on leaf litter decomposition and nutrient cycling are also moderated by nutrient regime, where nutrients exert a greater effect than does genotype (Madritch et al. 2006). In contrast, we observed that the effect of provenance on erosion resistance equaled or exceeded the effect of nutrients. Indeed, provenance explained twice as much of the observed variation in deep soil shear strength. It is possible, however, that greenhouse-scale measures do not adequately capture the full range of effects that nutrient enhancement may elicit.

Management implications

The fate of imperiled salt marshes in part depends on responses of *S. alterniflora* to elevated nutrient regimes (Deegan et al. 2012). Nutrient loading might reduce erosion by stimulating a net gain of BG biomass (Morris et al. 2013a,b). By lowering demand for foraging, nutrient loading might instead reduce BG growth (Darby & Turner 2008a,b). It might also weaken soil integrity by increasing rates of decomposition (Turner 2011). Since both productivity and soil characteristics are circumscribed by the extended phenotype of *S. alterniflora* (Seliskar et al. 2002, Bernik 2015), it is possible that marsh erosion is contingent on heritable and non-heritable variation in response to nutrient availability. Consistent with prior studies (Morris et al. 2013a), we found that nutrient addition resulted in greater biomass as well as changes in architecture that did not increase shoot:root ratios. Additionally, elevated nutrients resulted in increased surface elevation and higher erosion resistance. However, we found that traits that can govern erosion resistance (e.g. root:rhizome ratios, rhizome tensile strength) differed according to provenance, as did trait-specific responses to N enhancement that may reflect differences in resource allocation strategies. These findings suggest that out-

comes of coastal restoration projects, such as river diversions that aim to deliver sediment-rich but nutrient-laden freshwater to adjacent delta marshes (Morris et al. 2013a), may be contingent on the genetic composition of resident ecosystem engineers as much as, or more so, than prevailing environmental conditions. Thus it would be prudent to assess heritable and non-heritable responses of plants at candidate outfall locations to better understand potential outcomes of river diversions. Similarly, though we did not find evidence that cultivation of *S. alterniflora* for targeted traits has resulted in functional trade-offs that diminish erosion resistance, coastal restoration programs should nonetheless take precaution and evaluate whether cultivars achieve performance goals at sites targeted for use.

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