

Parthenocissus quinquefolia from coastal sand dunes are more tolerant than inland populations to salt spray, but neither sand burial nor seedling emergence in sand

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Abstract

Current standard practices of planting *Ammophila breviligulata* and other grasses to stabilize dunes on the North American Atlantic Coast, may be enhanced by the North American woody vine *Parthenocissus quinquefolia*. A series of five greenhouse experiments tested if there are ecotypes of *P. quinquefolia* that will perform better in coastal sand dune restoration using plants sampled from coastal and inland habitats. We tested the growth responses of potential ecotypes in response to common dune stressors: salt spray, sand burial, and germination in sand. Individuals sampled as vine cuttings and grown from seeds sampled from dunes showed higher tolerance to foliar salt spray treatment than those from inland habitats. Plants grown from seed sampled from dunes regrew thicker leaflets than those from inland habitats after defoliation. In response to sand burial, plant provenance had no effect. All *P. quinquefolia* vines treated with sand burial grew larger than those that received no sand treatment, indicating that burial stimulates growth. Seed provenance also had no effect on seed mass nor on seedling emergence when sown into beach sand. These results show that these responses to dune stressors are not related to seed provenance. Coastal land managers looking to improve habitat value of dunes by planting *P. quinquefolia* may not need to prioritize the use of dune ecotypes over inland sources.

Introduction

Enhancing dune plantings

Vegetation on dunes enhances shoreline protection (Sigren et al. 2018; Feagin et al. 2019) and creates valuable habitat (Nordstrom et al. 2011; Wootton et al. 2016; Johnston et al. 2023). *Parthenocissus quinquefolia* (L.) Planch, Virginia Creeper, is a berry-producing liana (Bush 2002). *P. quinquefolia* grow naturally on preserved coastal sand dunes and maritime forests in this region (Martin 1959; Graetzb 1973; Collins 1994), but due to human development many populations have been destroyed or degraded (Peterson 2019; Eastman 1992; Flint 1985).

In the Eastern United States, *Ammophila breviligulata*, American Beachgrass, is commonly planted as a monoculture to build and restore coastal sand dunes (Maun 2009). Occasionally, other grass species are added (Walker and Zinnert, 2022). Planting *P. quinquefolia* could improve restoration of sand dunes along this coast.

Increasing species richness on dunes will enhance the ecosystem services provided by those restoration plantings. Fruit from *Parthenocissus* species provide food for at least 27 species of bird across 11 genera (Martin et al. 1961). *P. quinquefolia* plants host at least 30 Lepidoptera species in the New Jersey Region (NWF 2020). Additionally, at least three mammals consume its fruit and foliage: *Vulpes vulpes*, *Sylvilagus floridanus*, and *Mephitis mephitis* (Martin et al. 1961). By contrast, *Ammophila* species provide habitat to less than half the bird, lepidoptera and mammal species that *Parthenocissus* supports.

Also, woody vines such as *P. quinquefolia* are easier to propagate than woody tree and shrub species (Hartmann et al. 2014). In addition to supporting habitat ecosystem services, adding biodiversity to the dunes will add cultural ecosystem services by enhancing the aesthetics of the planted area (TEEB 2011).

Obtaining resilient plant material

Plants on sand dunes must survive many stressors such as wind-driven sand and salt spray that can damage leaf tissue (Boyce 1954) and shifting sands that bury plant stems. These abiotic conditions may drive adaptations of *P. quinquefolia* dune populations. These populations may be considered dune ecotypes. “Ecotype” has had many definitions over the past century (Lowry 2012). Here the term is used to mean the nonrandom adaptation of a species in populations found growing in a specific habitat, in this case coastal sand dunes.

Isolated populations within a species can differ in genetic variation (Kawecki and Ebert 2004; Leimu et al. 2006; Briggs 2009), which has implications for where to sample plant material for ecological restoration projects (McDonald et al. 2016). The common standard for sampling plant material is typically “local is best,” but this standard has many interpretations and limitations that have been discussed widely (Millar and Libby 1989; McKay et al. 2005; Broadhurst et al. 2008; Mijnsbrugge et al. 2010; Breed et al. 2013; Jones 2013; Bucharova 2017; Breed et al. 2018; Dupré la Tour et al. 2020; McMullen 2022). Due to habitat fragmentation caused by human development, local populations to sample from may not be extant, or if existing, may be deficient in genetic variation causing bottlenecks (Briggs 2009; Bischoff et al. 2010; Jones 2013; Dupré la Tour et al. 2020; McMullen 2022; Leimu et al. 2006).

“Climate-adjusted provenancing” sources seed from habitats that share a similar climate to that predicted for the future (Breed et al. 2018; Prober et al. 2015; Dupré la Tour et al. 2020). “Assisted Gene Flow” where sampled populations are transplanted within their natural ranges is more widely accepted (Aitken and Whitlock 2013).

Restoration projects considering supplementing local populations with distant seed sources may encounter untested consequences of using non-local seed (Bucharova et al. 2016; Bucharova 2017). A meta-analysis of 74 studies found that about half of the studies showed local ecotypes were better adapted to local sites than those from non-local populations (Hereford 2009). In half of the experiments, no significant differences between local and foreign populations were detected.

This study of *P. quinquefolia* local adaptation to dune habitats tests the effect of salt spray, seedling emergence in sand, and sand burial.

Salt spray

Exposure to salt spray (Ehrenfeld 1990; Martin 1959) can inhibit the growth and development of plants (Sykes and Bastow 1988; Cheplick and Demetri 1999). Coastal plants have several strategies for limiting damage from salt spray. Plants can avoid salt spray by growing in protected niches shielded by dune sands or other vegetation. Many dune plant species grow low-to-the-ground, a prostrate habit to avoid salt spray (Maun 2009). Species sensitive to salt spray such as *P. quinquefolia* are able to grow near a high salt spray zone by growing close to the ground.

The second common strategy to avoid salt is exclusion of windborne salts through leaf fortification. This can include thick cuticle or epicuticular wax, and/or trichomes (Maun 2009). Coastal winds also carry sands

which can abrade leaf fortifications allowing salts to enter (Boyce 1954).

Sand Burial: Coastal dune plants must survive shifting sands fueled by wind erosion and accretion (Ehrenfeld 1990; Martin 1959). If *P. quinquefolia* is to be used in a coastal restoration strategy, it must be able to thrive in shifting sands. A dune can rise over a meter within a single growing season from windblown sand accretion (Wootton et al. 2016). Many dune plants respond to sand burial by increasing growth. Some coastal grasses (e.g., *A. breviligulata*) not only endure burial but require sand accumulation for survival (Martin 1959).

Seedling emergence

The sustainability of restoration projects requires subsequent generations to be able to establish after the initial planting and maintenance phases are complete. During this time even short periods of drought or sand burial will cause mortality (Maun 2009). Investigating this stage of development helps determine if there are significant differences in *P. quinquefolia* seeds sampled from dune and inland populations.

The following greenhouse trials with *P. quinquefolia* simulate stressors common to sand dunes: salt spray, sand burial, and seedling emergence in sand. Also, tests are done on intraspecific local adaptations affecting stress tolerance by *P. quinquefolia* sourced from two distinct environments: inland populations sampled from forest edges at least several kilometers from the coast and dune populations sampled from coastal sand dunes located within 150 meters of the Atlantic shore.

Materials and Methods

Plant material sampling locations

Plant material was sampled as either vine cuttings or berries with seeds from naturally occurring populations during July 2017 through July 2018 from New Jersey, Delaware, and Maryland (Fig. 1; Supplementary Materials). Sampling locations were classified as either “inland” or “coastal sand dune” based on distance from ocean and by soil traits (Table 1). Dune soils had a sand texture, low in organic matter and low electrical conductivity, a measure of soil salinity (Table 1). Local dune vegetation consisted primarily of *A. breviligulata*, other herbaceous plants and scattered patches of woody plants such as *Hudsonia tomentosa* and *M. pennsylvanica* in the dune hollows. Inland sites were all in New Jersey, 4–40 km from the ocean. Inland soils were loamy with more organic matter, lower pH and higher electrical conductivity than dune soils (Table 1). Inland plant material was sampled at woodland edges where forest patches transitioned to meadow or lawn. On coastal sand dunes, *P. quinquefolia* habitat is limited to behind the crest of primary dunes and not beachside.

Table 1

Soil conditions at plant material sampling locations Soil conditions as determined by Rutgers University Soil Lab analyses. Organic matter percentage determined by loss on ignition. Sampled Site codes: Assateague State Park, MD (AS); Barnegat Light, NJ (BL); Island Beach State Park, NJ (IB); Weltz Park, NJ (WP); Manasquan Reservoir, NJ (MR); Perrineville Lake Park, NJ (PL); Rutgers Gardens, NJ (RG); Hutcheson Memorial Forest, NJ (HF); Sourland Mountain, NJ (SM).

Sampling Area Classification			Soil Traits					
Site	Physiographic region	Provenance	Texture	Organic matter (%)	EC (mmho/cm)	pH	Nitrogen (%)	Carbon (%)
AS	Coastal Plain	Dune	Sand	0.28	0.04	5.86	0.0070	0.12
BL	Coastal Plain	Dune	Sand	0.20	0.04	6.29	0.0070	0.09
IB	Coastal Plain	Dune	Sand	0.08	0.03	6.41	0.0020	0.02
WP	Coastal Plain	Inland	Loamy Sand	2.96	0.06	5.54	0.0940	1.38
MR	Coastal Plain	Inland	Loamy Sand	4.28	0.17	5.41	0.1480	2.14
PL	Coastal Plain	Inland	Sandy Loam	5.46	0.13	5.45	0.2840	3.14
RG	Piedmont	Inland	Clay Loam	6.67	0.18	4.89	0.1580	2.45
HF	Piedmont	Inland	Loam	4.73	NA	5.80	NA	NA
SM	Piedmont	Inland	Silt Loam	6.37	0.08	5.50	0.1890	2.26

When sampling from a vine patch, it is not possible to determine if samples came from a single *P. quinquefolia* or multiple plants growing together in a multi-branched, tangled patch. Consequently, when classifying plant material sources, the smallest unit of measurement is “vine patch” defined as a single group of vines growing together with clear borders. A single patch was classified as distinct from adjacent patches if there was no above ground *P. quinquefolia* for at least 20 m between patches. A single vine patch is likely to be either a large individual or several closely related individuals. However, *P. quinquefolia* is bird dispersed (Henson 2005), so individual plants within a patch could be genetically distant. “Vine patch” is our closest approximation to a single “genotype” of *P. quinquefolia*. Experiments tested multiple plants sampled from the same vine patches. Data were analyzed hierarchically to account for this nesting within habitat type.

Seed processing

Fruit was sampled in late summer and fall when berries were blue-black and tender. Seeds were separated from berry flesh, dried, then stored in glass jars at 4°C with silica gel packets to maintain dryness. As *P. quinquefolia* seeds are bird dispersed, they were scarified with fine sandpaper to imitate the digestion process through a bird gizzard. We then soaked seeds for 24 hours in distilled water, strained them, and cold

stratified seeds at 4°C for 80 days in sphagnum moss. Seeds then were sown into SunGro™ potting mix at a 1 cm depth.

Salt spray tolerance

Seawater for foliar salt spray was from Corson's Inlet, Ocean City, New Jersey, supplied on the incoming near-high tide to best assure full-salinity. The seawater was filtered, then passed through 1 µm string wound cartridge filters before use. Seawater salinity was 34 mg/mL, measured by refractometer. In our greenhouse experiments of effect of foliar salt spray, plants were sprayed with approximately 7 mL of this ocean water each day. This exposed plants to more salt than typically experienced on coastal sand dunes.

To measure natural salt spray exposure, we deployed 79 salt traps 1–10 cm above the sand surface where dune populations of *P. quinquefolia* were located. Traps were made of cheesecloth stretched over a frame, installed parallel to the shore, and left out for a 24-hour period (Fig. 2). Tests were at Delaware Seashore State Park, Island Beach State Park, and Assateague State Park dunes. Salt was measured by cutting a 10 cm square of the cloth, soaking it in 100 mL of deionized water and measuring the concentration of chloride with an ion-selective electrode.

Foliar salt spray tolerance was tested in two greenhouse experiments. The first tested the response to foliar spray of 70 *P. quinquefolia* leaflets on plants grown from 30 vine cuttings from seven vine patches in inland habitats and 40 from ten vine patches in dune habitats (see Supplementary Materials for locations). After sampling, vines were stripped of leaves, randomized in 3.8 L containers of SunGro™ potting mix, and grown in a greenhouse for one year while growing new leaves. We covered the top openings of pots with plastic to block foliar salt spray from entering the root zone, limiting the test to the response of foliage to salt spray, not root tolerance to salt (Fig. 3).

The number of leaflets with at least 2 cm² of green surface area on the lower 50 cm of each potted vine were counted before treatment, and again after one and two weeks of daily foliar salt spray. We calculated the Leaflet Relative Change (LRC) for each plant. LRC was compared between plants of dune and inland provenance at one and two weeks (time_t) of foliar salt spray.

$$\text{LRC} = (\text{No. leaflets time}_t - \text{No. leaflets time}_0) / (\text{No. leaflets time}_0)$$

The second foliar salt spray experiment tested vines grown from seed, not cuttings, sampled from the inland and coastal environments. 90 plants were grown from seed sampled from six vine patches on dunes and 75 plants grown from seed sampled from five vine patches at inland habitats (see Supplementary Materials for locations). We modified the experimental design by including an additional 50 dune and inland plants that were sprayed with tap water each time the salt treatment group was sprayed with ocean water. This would control for changes in leaf area that may be due to greenhouse factors other than salt spray. Instead of counting the leaflets on each test plant, we calculated a Leaf Area Estimate (LAE). LAE accounted for variation in leaflet size. Leaflet size was classified by length from leaflet base to apex as: small (< 2 cm), medium (2–5 cm) and large (> 5 cm):

$LAE = (\text{No. small}) + (2 * \text{No. medium}) + (4 * \text{No. large})$

One-meter-long portions of vine stem with foliage were tied with jute string across two half-meter stakes to form an arch to standardize the tested portions of these vines. Growing tips were tucked beneath plastic wrap and not part of the measured leaf area. Plants of each provenance were randomized in rows. Plants were treated with foliar spray daily for three weeks. LAE was measured prior to treatment and weekly during treatment to calculate the Relative Change in Leaf Area (RCLA).

$RCLA = (LAE_{\text{time}} - LAE_{\text{time}}) / (LAE_{\text{time}})$

We measured leaflet thickness to 0.1 mm with a digital caliper to determine thickness as a potential mechanism for preventing salts from entering leaves. Four leaves per plant were measured, with two measurements taken from the upper, central leaflet. Measurements were at the midpoint of the leaflet in the lamina between veins on either side of the midvein. The mean of these eight measurements provided a value for each potted vine. Mean leaf thickness was recorded before salt and tap water treatments. After the treatment period, any remaining foliage was removed from every plant. Plants were allowed to re-grow foliage for six weeks after defoliation, then LAE and leaflet thickness were re-measured.

Statistical analyses

To determine if experimental treatment and provenance of plant material influenced measured responses, mixed models were implemented as Linear Mixed Models (LMER) in R (version 4.0.3; 2020-10-10). The plants tested were categorized as either dune or inland provenance. Provenance was nested, with “dune” and “inland” as higher-level categories (fixed effect) and “Sampled Vine Patch” as a nested lower-level category (random effect). For mixed models we calculated the Intraclass Correlation Coefficient (ICC) to determine the proportion of the total variability in the outcome attributable to the random effect of sampled vine patch (Lorah 2018; Monsalves et al. 2020). The outcomes for each model were the measured responses: LRC and RCLA. These dependent variables were predicted by the categorical variables of treatment and provenance. Data measured in salt spray experiments were collected weekly, so weighted least squares were included in these models to compensate for variances that were clustered around each week (Kunert, 1985). Weekly salt spray data included individual test subject (single potted vine) as an additional random effect in the mixed model. Post hoc tests comparing estimated marginal means, or least square means were performed with the emmeans package in R. Provenance contrasts were compared at each measured week for the salt spray experiments.

Pre-treatment mean leaflet thickness was compared between all plants of dune and inland provenance by a t-test and whether or not plants regrew their leaves was tested with Fischer’s exact test of binary variables (Field et al. 2012). Of the plants that regrew their leaves after defoliation, those previously treated with salt or tap water were analyzed with Analysis of Covariance (ANCOVA) to test if plant provenance impacted leaflet thickness of the newly grown leaves (Field et al. 2012). ANCOVA models included two covariates. The leaf area estimates of regrown leaves post-defoliation covariate accounted for variations in plant size of plants that re-grew after treatment, and the pre-treatment leaflet thickness covariate accounted for differences in leaflet thickness prior to treatment. Effect size of each variable was calculated with partial eta squared (*partial η^2*).

Sand burials

Two greenhouse experiments tested the growth in response to sand burial. The first test exposed vines to a gradual sand burial treatment meant to simulate daily sand accretions. The second test simulated a major storm event by completely burying the plants with a large sudden sand burial treatment. In both experiments, half of the plants were left untreated, as a control, with no sand burial.

Plants were grown from stratified seed and sown into standard grow mix filled nursery trays in October 2019. Three months later, vine length and estimates of leaf area were recorded for each seedling, then they were individually potted and randomized by treatment and seed provenance on greenhouse tables. Plants were acclimated for one week prior to treatment. Plant size was re-measured after the treatments to determine overall change in growth. Sand was sourced from Seven Presidents Oceanfront Park, Monmouth County, NJ, then dried and passed through a number 10 sieve. Throughout the treatment periods, plants were watered once per week.

The gradual burial experiment included 399 *P. quinquefolia* plants and transplanted into clear growth tubes (Fig. 4). 120 seedlings from six vine patches in dune habitats were treated with gradual sand burial and 119 dune plants were untreated. 79 seedlings from four inland vine patches received the sudden sand burial treatment, and 81 inland plants were untreated. Actively growing sand dunes can increase between 8–120 cm per year (Maun 1998). We added sand at a rate toward the higher end of this range at a rate of 2.2 cm per week. Gradual sand burial treatment was administered as 1/3 cup of sand poured into growth tubes twice a week for five weeks. Total added sand depth from gradual sand burial treatment was 11 cm (± 2 cm) at time of harvest. Plant measurements of leaf area estimates and stem length were recorded one week prior to treatments and one week after the final sand burial treatment. The relative change in leaf area estimate and stem length were calculated from these two measurements. Differences between these measured responses were compared between gradual sand treatment and no sand treatment and between provenance within those two treatment groups.

The sudden burial trial included 196 plants. 105 of the plants (60 of dune and 45 of inland provenance) received a one-time treatment of 12 cm of sand. The remaining plants (50 of dune and 41 of inland provenance) were left to grow in tubes with no sand added. Dune plants in both treatment groups were grown from seed sampled from the same four dune vine patches as were inland plants sampled from three inland vine patches. 50 days after the sudden burial treatment, plants were harvested, then stem length and leaf area estimate were recorded. Differences between these measured responses were compared between sudden sand burial and no sand treatments and between provenances within those two treatment groups.

Sand burial experiments had two growth measurements, vine length and LAE. To reduce type II error, these two dependent variables were first tested with Multivariate Analysis of Variance (MANOVA) and if a significant result was detected, further testing with mixed models for each measured response were created (Field et al. 2012). A t-test was used to detect an effect of sand treatment alone, without provenance included in the model. Survival and emergence recorded in the sudden sand burial experiment were binary responses. Treatment and provenance groups were compared with Fisher's exact test for binary variables.

Seedling Emergence

To examine the effect of substrate, we compared seedling emergence rates of seeds sampled from dune and inland environments when sown into either beach sand or Sunagro™ growing mix comprised of peat moss and perlite. Seeds were sampled from 11 vine patches from dune habitat and seven inland vine patches (Fig. 1 **Error! Reference source not found.**). Beach sand was from Island Beach State Park, NJ, then dried and passed through a number 10 sieve to remove any debris or particles larger than 2mm. Prior to planting, we measured the mass of 200 dry seeds from each sampled vine patch to determine if seed mass was related to provenance. Sample sizes of seeds sown were unequal (Grow Mix, $n = 1350$; Sand, $n = 771$), but each growing media contained seeds from the same vine patches for direct comparisons. Seeds within each treatment were sown at a 1 cm depth and randomized within planting trays. Grow mix was contained in 48-cell plastic nursey trays, while sand was contained in 6 cm diameter fabric grow bags (Fig. 5). The fabric bags allowed the sand to dry out more than solid plastic trays, a choice made to add stress on emerging seedlings. Trays and bags were heavily watered once per week throughout the experiment. The fabric growbags allowed the sand surface to dry out more often than the potting mix in plastic cells, but the sandbags never dried out during the experiment; the bottoms were consistently moist in between waterings.

The number of seedlings emerging were recorded at 20- and 40-days post-sowing for both studies and were analyzed to test if growing media and containers or seed provenance impacted seedling emergence rates. To analyze the effect of growing conditions and plant provenance on the binary response variable of seedling emergence, logistic mixed regression models was used (Sommet and Morselli 2017) with growing media treatment and provenance as fixed effects, sampled vine patch as a random effect.

Results

Salt spray test on vine cuttings

The salt trap measurements (Table 2), $M = 26.4$ mg/mL; $SD = 102.1$, were comparable those found in other coastal salt sprays (Maun 2009; Martin 1959). Consequently, the dune plants used for seed and cuttings in the following experiments originated in typical salt spray environments.

Table 2
Salt trap measurements of chloride concentration on dunes. Salt trapped within

Site (Number of traps)	Date	Mean Cl ⁻ (mg / mL)	SE
Island Beach State Park, NJ (52 traps)	July 13, 2018	13.9	1.5
Delaware Seashore State Park, DE (37 traps)	June 18, 2018	19.0	1.8
Assateague State Park, MD (6 traps)	July 26, 2017	263.6	121.9
a square decimeter of cloth from salt traps deployed for 24 hours over coastal sand dunes where <i>Parthenocissus quinquefolia</i> were found growing. Accumulated salt was estimated by chloride ion concentration. The number of traps at each site varied from six to 52.			

Samples from dune environments lost fewer leaflets than those from inland environments (Fig. 6). The fixed effect of “Provenance” predicted LRC after one and two weeks of salt spray treatment, $t(60.6) = 2.17, p = .03$; $t(55.5) = 2.34, p = .02$; respectively (Table 3). Random effects of sampled patch and test subject had little effect on the outcome, ICC = 0.3.

Table 3
Leaflet Relative Change from salt spray predicted by provenance of vine cutting

A mixed model of coefficients and confidence intervals of fixed effects (Provenance) is included in the table. The model also used sampled vine patch and individual plant tested as random effects. Asterisk denotes coefficients with significant effect at 95% confidence levels.				
Week	Provenance	<i>b</i> (mean LRC)	SE <i>b</i>	95% CI
1	Dune	0.04	0.05	0.039, 0.046*
	Inland	-0.14	0.06	-0.138, -0.129*
2	Dune	-0.42	0.05	-0.425, -0.414*
	Inland	-0.63	0.06	-0.630, -0.591*

Salt spray test on seed grown plants

Foliar salt spray reduced Leaflet Area Estimates on salt treated plants more than those treated with tap water. Plants grown from seed sampled from dune environments suffered less loss in LAE than those from inland environments (Table 4). The fixed effects of “Treatment” and “Provenance” significantly impacted RCLA after one and two weeks of salt spray treatment, but not at three weeks of treatment, $t(36.5) = 2.09, p = .04$; $t(38.5) = 2.86, p = .007$; $t(39.2) = 0.61, p = .5$; respectively (Fig. 7). At three weeks all plants were severely damaged from salt spray, with 70% of salt treated plants having lost all leaflets. Random effects of sampled patch and test subject had little effect on the outcome, ICC = 0.3.

Table 4

Mixed models of mean Relative Change in Leaf Area (RCLA) testing if plant provenance of seed grown plants and spray treatment (salt or tap water) predict leaf response. Provenance and Treatment are fixed effects and both individual sampled plants and individual tested plants as random effects in the mixed model. Asterisk denotes coefficients with significant effect at 95% confidence intervals.

Week	Treatment	Provenance	<i>b</i> (mean RCLA)	<i>SE b</i>	95% CI
1	Salt Spray	Dune	-0.26	0.03	-0.258, -0.257*
		Inland	-0.35	0.03	-0.346, -0.345*
	Tap Water	Dune	-0.06	0.04	-0.063, -0.061*
		Inland	-0.10	0.05	-0.099, -0.097*
2	Salt Spray	Dune	-0.65	0.03	-0.652, -0.651*
		Inland	-0.78	0.03	-0.778, -0.777*
	Tap Water	Dune	-0.05	0.04	-0.049, -0.048*
		Inland	-0.13	0.05	-0.132, -0.130*
3	Salt Spray	Dune	-0.96	0.03	-0.959, -0.958*
		Inland	-0.99	0.03	-0.986, -0.985*
	Tap Water	Dune	-0.06	0.04	-0.061, -0.060*
		Inland	-0.15	0.05	-0.153, -0.151*

Prior to treatment, there was no difference in mean leaflet thickness between plants of inland ($M = 0.157$ mm; $SD = 0.021$) or dune ($M = 0.155$ mm; $SD = 0.019$) provenance, $t(191) = -0.56$, $p = .6$, $d = 0.07$. Six weeks after defoliation 154 of the 215 plants tested had regrown their leaves. Provenance had no effect on whether a plant regrew leaves (Fishers exact test of binary variables, $p = .7$). Leaflet thickness of regrown leaves on all plants ($M = 0.138$ mm; $SD = 0.020$) was less than pre-treatment leaflet thickness ($M = 0.156$ mm; $SD = 0.020$). Provenance had a significant effect on leaflet thickness of newly regrown foliage. Those from dunes were significantly thicker ($M = 0.14$ mm; $SD = 0.018$) than inland plants ($M = 0.13$ mm; $SD = 0.021$), $F(1) = 7.37$, $p = .007$, $partial \eta^2 = 0.05$. Plant size, measured in LAE of regrown leaves, had a larger significant effect on leaflet thickness, $F(1) = 17.06$, $p < .0001$, $partial \eta^2 = 0.11$, than provenance ($partial \eta^2 = 0.05$). Post treatment leaflet thickness of regrown leaves is correlated with LAE of regrown leaves, $R^2 = 0.1$, $F(1,146) = 16.43$, $p < .0001$. There was no difference in LAE of regrown leaves from dune ($M = 236.1$ cm²; $SD = 118.8$) and inland plants ($M = 236.9$ cm²; $SD = 131.7$), $t(123) = -0.04$, $p = .9$, $d = 0.007$. Neither water treatment type nor pre-treatment leaflet thickness had an effect on post treatment leaflet thickness, $F(1) = 0.06$, $p = .8$, $partial \eta^2 = 0.0004$; $F(1) = 0.56$, $p = .5$, $partial \eta^2 = 0.004$, respectively.

Gradual sand burial

After treatment, plants experiencing gradual sand burial were larger than those with no sand added (Fig. 8). Mean stem length of all plants measured 3.4 cm ($SD = 1.2$) before treatment. After treatment with gradual

sand, stem length ranged from 3.5–153.4 cm and 3.4–108.4 cm in the control group that received no sand. Plants gradually buried in sand had greater Leaf Area Estimates (LAE) ($M = 117 \text{ cm}^2$; $SD = 65.2$) than those with no sand treatment ($M = 93 \text{ cm}^2$; $SD = 45.9$), $t(355) = 4.28$, $p < .0001$. Likewise, those gradually buried in sand had longer stem lengths ($M = 63 \text{ cm}$; $SD = 28.2$) than those with no sand treatment ($M = 35 \text{ cm}$; $SD = 22.7$), $t(378) = 10.77$, $p < .0001$. A MANOVA of change in plant size predicted by sand treatment and plant provenance showed significant effects (Table 5), indicating a need for further testing of each measured response separately (Table 6). In Tukey p -adjusted post hoc contrasts of mixed linear models, neither treatment nor provenance influenced the change in leaf area estimates between groups, but treatment did significantly affect change in vine length (Error! Reference source not found.9).

Table 5

Change in stem length and leaf area in response to gradual sand burial. A two-way MANOVA comparing multiple dependent variables of mean change in leaf area and mean change in vine length with sand treatment and provenance as predictors. Treatment and provenance were both significantly different, indicating a need for further testing of each plant part separately. Plants were treated with gradual sand burial, or no sand added in a greenhouse setting. Asterix on significant p -values.

MANOVA	DF(num,den)	Pillai (V)	f	p
Gradual Sand Treatment	(2,395)	0.14	31.66	< .0001*
Plant Provenance	(2,395)	0.03	6.76	.0001*

Table 6

Change in plant size predicted by gradual sand burial and plant provenance. A table of parameters from mixed models testing if plant provenance predicts biomass of individual plant parts with provenance as fixed effects and individual vine patches where seeds were sampled from in the field as random effects. Asterisk denotes coefficients with significant effect at 95% confidence intervals. Mean change in relative leaf area estimates and vine length, M , has no units because it is a relative change calculation.

Relative Change in:	Treatment	Provenance	M	b	$SE\ b$	95% CI
Leaf Area Estimate	Gradual Sand	Dune	5.17	5.17	0.96	3.35, 6.99*
		Inland	6.09	0.97	1.51	-1.92, 3.86
	No Sand Added	Dune	4.23	-0.93	0.91	-2.72, 0.86
		Inland	8.50	3.29	1.51	0.41, 6.17
Vine Length	Gradual Sand	Dune	19.20	19.20	1.44	16.45, 21.96*
		Inland	17.65	-1.51	2.28	-5.87, 2.86
	No Sand Added	Dune	10.29	-8.93	1.30	-11.47, -6.37*
		Inland	11.99	-7.25	2.28	-11.60, -2.90*

Table 7

Plant size in response to sudden sand burial A two-way MANOVA comparing two dependent variables of mean change in leaf area and mean change in vine length. Dependent variables predicted by response to sudden sand burial treatment and provenance as independent variables. Treatment, but not provenance, was a significant predictor of plant size, indicating a need for further testing of each plant part separately. Asterix on significant p-values.

MANOVA	DF (num,den)	Pillai (V)	f	p
Sudden Sand Treatment	(2,192)	0.081	8.44	.0003*
Plant Provenance	(2,192)	0.004	0.43	

Sudden sand burial

Before sand treatment, mean stem length for all *P. quinquefolia* to be tested was 4.1 cm ($SD = 1.5$). After the treatment period, stem length ranged from 3.3–49.7 cm in plants treated with sudden sand burial and 3.4–49.0 cm in control groups having no sand added. MANOVA test indicated sand treatment may have a significant effect on plant size (Table 8). Follow-up testing with a t-test showed a small positive effect of sand burial on stem length, but not LAE, $t(192) = -2.08$, $p = .04$, $d = 0.3$; $t(191) = 1.56$, $p = .1$, respectively. Plants buried with sudden sand treatment had a greater relative change in vine length ($M = 2.8$; $SD = 2.3$) than those that received no sand treatment ($M = 2.2$; $SD = 2.2$). When provenance was included in mixed models, post hoc contrast testing showed no effect from treatment nor provenance on relative change in LAE or vine length (Table 9). There was no plant mortality in those treated with sand, but 8 of 91 plants in the control group (no sand) died during treatment. A significant difference in mortality was detected by Fisher's exact test for binary variables, $p = .002$. Provenance had no effect on plant survival in the control group mortality, $p = .3$. Of the 105 plants that received sand burial 57% grew enough to emerge above the sand within 50 days of receiving treatment. Provenance had no effect on emergence from sudden sand burial, $p = .2$.

Table 8

Plant size in response to seed provenance and sudden sand burial. Parameters from mixed models testing if plant provenance and sudden sand burial treatment significantly predicts relative change in leaf area estimate or vine length. Provenance and sudden sand burial are fixed effects and random effect is the sampled vine patch which provided seeds to grow plants tested. Asterisk denotes coefficients with significant effect through 95% confidence intervals. Mean change in leaf area estimates and vine length (*M*) has no units because it is a relative change calculation between the same individual plants measured before and after the treatment period.

Relative Change in:	Treatment	Provenance	<i>M</i>	<i>b</i>	<i>SE b</i>	95% CI
Leaf Area Estimate	Sudden Burial	Dune	0.43	-0.46	0.26	-0.97, 0.04
		Inland	0.67	-0.21	0.28	-0.76, 0.33
	No Sand Added	Dune	0.89	0.89	0.19	0.51, 1.26
		Inland	0.76	-0.13	0.29	-0.69, 0.42
Vine Length	Sudden Burial	Dune	2.76	0.31	0.43	-0.52, 1.14
		Inland	2.98	0.52	0.64	-0.67, 1.71
	No Sand Added	Dune	2.43	2.45	0.43	1.65, 3.25*
		Inland	1.86	-0.59	0.64	-1.80, 0.62

Table 9

Seedling emergence predicted by growing media and provenance. In the seedling emergence experiment, seeds from the same sampled vine patches were sown into two different growing media and emergence was recorded 20 and 40 days after seeds were sown. Treatment and Provenance were fixed effects in GLMER models of binary response data and sampled vine patch was the random effect in the model. Asterix denotes significant coefficient effects with 95% confidence interval.

Days	Treatment	Provenance	<i>b</i>	<i>SE b</i>	<i>z</i>	<i>p</i>	Odds ratio	95% CI
20	Sand	Dune	-0.98	0.26	-3.69	.0002	0.38	0.22, 0.65*
		Inland	0.21	0.43	0.49	.6	1.23	0.53, 2.96
	Grow Mix	Dune	0.20	0.13	1.54	.1	1.22	0.95, 1.58
		Inland	0.84	0.41	2.03	.04	2.32	0.98, 5.45
40	Sand	Dune	0.07	0.19	0.39	.7	1.07	0.73, 1.57
		Inland	-0.24	0.30	-0.79	.4	0.79	0.42, 1.46
	Grow Mix	Dune	1.18	0.13	9.15	< .0001	3.27	2.54, 4.22*
		Inland	1.00	0.29	3.40	.0006	2.73	1.49, 5.01*

Seedling Emergence

Mean seed mass of a single *P. quinquefolia* seed was 17.4 mg (*SD* = 3.8). Seed provenance had no effect on seed mass in a simple t-test, $t(9.25) = 0.45$, $p = .7$. Mixed models including collection site as a random effect did not improve the fit of the seed mass model, allowing for the use of the simple t-test. When sown into

standard grow mix, seeds had higher rates of emergence than those sown into sand (Table 9). There was a difference in seedling emergence between types of growing media 20 days after sowing seed (Sand $M = 0.31$, $SE = 0.01$; Grow Mix $M = 0.43$, $SE = 0.01$; $t(1693) = -5.48$, $p < .0001$, $r = 0.25$) and increased effect on emergence between growing media 40 days after sowing (Sand $M = 0.51$, $SE = 0.02$; Grow Mix $M = 0.76$, $SE = 0.01$; $t(1398) = -11.84$, $p < .0001$, $r = 0.55$). While growing media treatment impacted results, seed provenance had no effect on emergence (Figure). Adding random effects of data nested within sampled vine patch increased the power of mixed models above simple logistic regression models, but variance from the random effect contributed very little to the seedling emergence model (Day 20 ICC = 0.18; Day 40 ICC = 0.08). Seed provenance still had no effect on emergence in the mixed models (Table 9).

Discussion

The results of these five experiments using the dune stressors of foliar salt spray, sand burial and seedling emergence in sand, determined that *P. quinquefolia* is likely to survive those stresses. Dune sourced populations outperformed inland populations in response to foliar salt spray, but provenance made no difference in plant responses to neither sand burial or to seedling emergence.

Salt spray

Both vine cuttings and plants grown from seed sampled from dune environments showed greater tolerance to foliar salt spray. Plants were treated with a salt spray volume and frequency many times greater than what plants would experience on a coastal sand dune. Almost all plants in the salt treatment were completely defoliated after treatment. Defoliation in response to salt stress is a strategy also utilized by *T. radicans* which shares a niche with *P. quinquefolia* on the dunes (Maun 2009).

In the tests of seed-derived plants we also measured leaflet thickness as a potential mechanism of salt tolerance. There was no effect of provenance on leaflet thickness prior to treatment, but there was a difference after leaves were regrown following post-treatment defoliation. All regrown leaves were thinner than measurements prior to treatment. This is likely due to leaf age, which was several months old prior to treatment and at most only six weeks old after defoliation. Treatment, whether salt or tap water, had no effect on thickness of regrown leaves, but provenance did. Plants of dune origin had thicker leaves than those from inland habitats. Defoliation possibly activated the response to grow thicker leaves in dune plants that was not present in *P. quinquefolia* from inland habitats. This rebound from defoliation stress could be a beneficial adaptation to the dune environment where sand abrasion and salt spray can damage leaves.

Foliar salt tolerance and leaf thickness were also studied in dune populations of *S. sempervirens* (Cartica and Quinn 1980; 1982). In the field, ocean facing populations of *S. sempervirens* had thicker leaves than landward plants growing only a few meters inland, on the back side of the dune. However, *S. sempervirens* grown from rootstocks had no difference in leaf thickness when grown under uniform greenhouse conditions.

Regardless of plant origin, when exposed to increasing levels of salt spray in the greenhouse, leaves thickened proportionally, indicating leaf thickness to be a phenotypically plastic trait. When sprayed with salt water, genotypes from inland *S. sempervirens* rootstock suffered more leaf damage than those sampled

closer to the shore (Cartica and Quinn 1980). The present study, where stem cuttings from dunes showed greater tolerance, opens the question of whether tolerance mechanisms are inherited. This cannot be answered by testing vegetatively propagated material. The salt tolerant phenotype expressed in cuttings sampled from dunes could have been activated by salt exposure during its life on the dunes and maintained after plants were placed in the greenhouse. A follow-up study could test if that same response could be activated in cuttings sampled from inland populations.

In tests of seed derived plants, there was a similar response of salt tolerant foliage on plants of dune provenance. Based on these results of seed grown plants, there is more confidence that there can be a heritable adaptation to abiotic conditions of sand dunes. Subsequent generations of *P. quinquefolia* should be tested to determine mechanisms of heritability.

Species with distinct coastal ecotypes have been studied around the world (Lowry 2012; Zambiasi and Lowry, 2024). Coastal ecotypes tend to have short stature, prostrate growth, thicker leaves, and flower later than counterparts inland (Lowry 2012). Dune populations of *P. quinquefolia* share some of these traits. Given the opportunity, *P. quinquefolia* vine will climb vertical structures, but on sand dunes where there is little opportunity, they grow prostrate. This benefits the plants by avoiding some sand abrasion and salt deposition. The leaf thickness data show dune vines produced thicker leaves than inland vines in response to salt spray stress. Future studies of salt spray induced *P. quinquefolia* leaflet thickness should include closer monitoring of post-defoliation leaflet growth. These studies did not monitor when plants re-grew their leaves during the six-week recovery period, but it is likely that dune leaflets were thicker because they were older. LAE of regrown leaves was greater for dune plants than inland plants, which could be because dune leaves re-grew faster than inland leaves. Faster regrowth of lost leaves, in addition to greater tolerance to salt spray, is consistent with these populations of *P. quinquefolia* being adapted to dunes.

Sand Burial

To survive sand burial, plants won't merely cope but will respond with greater growth and fecundity to sand accumulation. In these experiments of both gradual and sudden sand burial, *P. quinquefolia* responded by increasing growth, regardless of plant provenance. Growth was greater in response to partial sand burial than sudden burial. Gradual partial burial stimulates growth, but at a higher threshold, burial reduces growth. This response is found in other species tested with sand burial. In a study of dune grasses, growth was stimulated when plants were partially buried in 5–20 cm of sand, but growth was slowed at depths greater than 20 cm (Maun 1998). In this *P. quinquefolia* sudden burial experiment, seedlings were shorter than typical dune grasses and were completely buried by the 12 cm sand treatment. By the end of the treatment period over half were able to emerge beyond the sand depth. *P. quinquefolia* not only survived but had enhanced growth in response to burial.

Maun (2009) writes that of all the stressful abiotic conditions a plant must overcome to grow on a coastal sand dune, sand burial is the most limiting to species trying to colonize the habitat. Despite this study's results showing variation in foliar salt spray tolerance between *P. quinquefolia* of dune and inland provenance, there was no provenance relationship in response to sand burial. Therefore, *P. quinquefolia* sampled from either dune or inland environments could be considered for coastal dune restoration plantings. If resource

limited dune managers wish to include *P. quinquefolia* in planting projects, they may consider sampling local plant material from wherever it is readily available, regardless of habitat (Gage and Handel 2026).

Seedling Emergence

We found no differences in seed mass or seedling emergence of *P. quinquefolia* sampled from dunes and inland habitats. Moisture content available for the test plants was likely higher than those found on a dune, and further study should measure seedling emergence beyond the greenhouse, on a coastal sand dune. However, for this first investigation, the controlled conditions of the greenhouse were chosen out of concern that mortality in the field would be too high to statistically compare seedlings by provenance.

Seeds dispersed naturally to a coastal sand dune end up at varying depths because of the dynamics of shifting dune sands. For uniformity, we only tested seedling emergence of seeds sown 1 cm into substrate, but winter sand accumulations on a dune could be much greater. Seed mass is positively correlated with the distance beneath the sand's surface from which a seedling can emerge (Barbour et al. 1985).

This study found no difference in seed mass between *P. quinquefolia* seeds sampled from dune and inland habitats. We also found no difference in seedling emergence rates between seed of dune or inland provenance. The fact that *P. quinquefolia* seeds were able to emerge from beach sand, regardless of provenance, supports the potential of *P. quinquefolia* plantings at coastal restoration sites to successfully establish for future generations (Gage 2023). *P. quinquefolia* is a perennial vine

Bush with the potential to grow stems longer than 15 m (Henson 2005). Consequently, even if seedling recruitment at the dunes is low, planted vines can produce significant ground cover through vegetative expansion.

Conclusion

The results indicate that both plants sampled vegetatively and first generation propagates grown from seed, sampled from dune habitats will be more tolerant to salt spray stress than those from inland populations. While significantly more tolerant than inland plants, plants from dunes were still harmed by saltwater spray and this increased tolerance might not always translate to meaningful differences when planted in dune fields. Based on salt spray tolerance, *P. quinquefolia* propagated from dune populations would be preferred accessions for coastal restoration projects. Similarly, native plant nurseries should consider propagating dune ecotypes of *P. quinquefolia* with salt tolerant foliage for municipalities and residents to obtain for beach landscaping (Handel et al. 1994). These potential dune ecotypes should be prioritized for restoration plantings on coastal sand dunes. However, if fewer or no local dune populations are available, use of local inland populations, if more readily available would still be successful for dune restoration. *P. quinquefolia* grows low across the sand in areas of the primary dune that are protected from the high levels of salt spray that they received in these experiments. After salt spray defoliation, dune plants regrew their leaves faster, but there was no difference between dune and inland plants on whether they regrew leaves. Despite showing different levels of foliar salt tolerance, *P. quinquefolia* from both inland and dune populations should be able to withstand the periodic salt spray stress of the dune fields if planted behind the crest of the primary dune.

There, direct salt spray exposure is lower than ocean-facing side of the dune. Additionally, plants from both inland and dune populations showed equal phenotypic plasticity in response to sand burial and seedling emergence experiments. This is further evidence that *P. quinquefolia* sampled from inland areas may perform equally to those sampled from the dunes when planted for dune restoration.

Coastal sand dunes protect property against destructive storm surges (Woodhouse, 1978; Wootton et al., 2016; Nordstrom et al. 2022). They also support many wildlife groups, with special value during migrations. Addition of fleshy fruited plants such as *P. quinquefolia* adds to the ecosystem value of dunes, complementing the erosion control value of graminoids, the typical treatment at these sites.

Declarations

Supplementary Material

The online version contains supplementary material available at <https://doi.org/xxxxxxx>

Declarations

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This research is for all the restoration crews working to better our natural areas.

Author Contribution

Both authors contributed to the study conception and design. A.S.G. performed the data collection and analyses and wrote the first draft of the manuscript. S.H. prepared the final manuscript, which both authors read and approved.

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Data Availability

The data that support the findings of this study are not openly available but are available from the corresponding author upon reasonable request.

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Figures

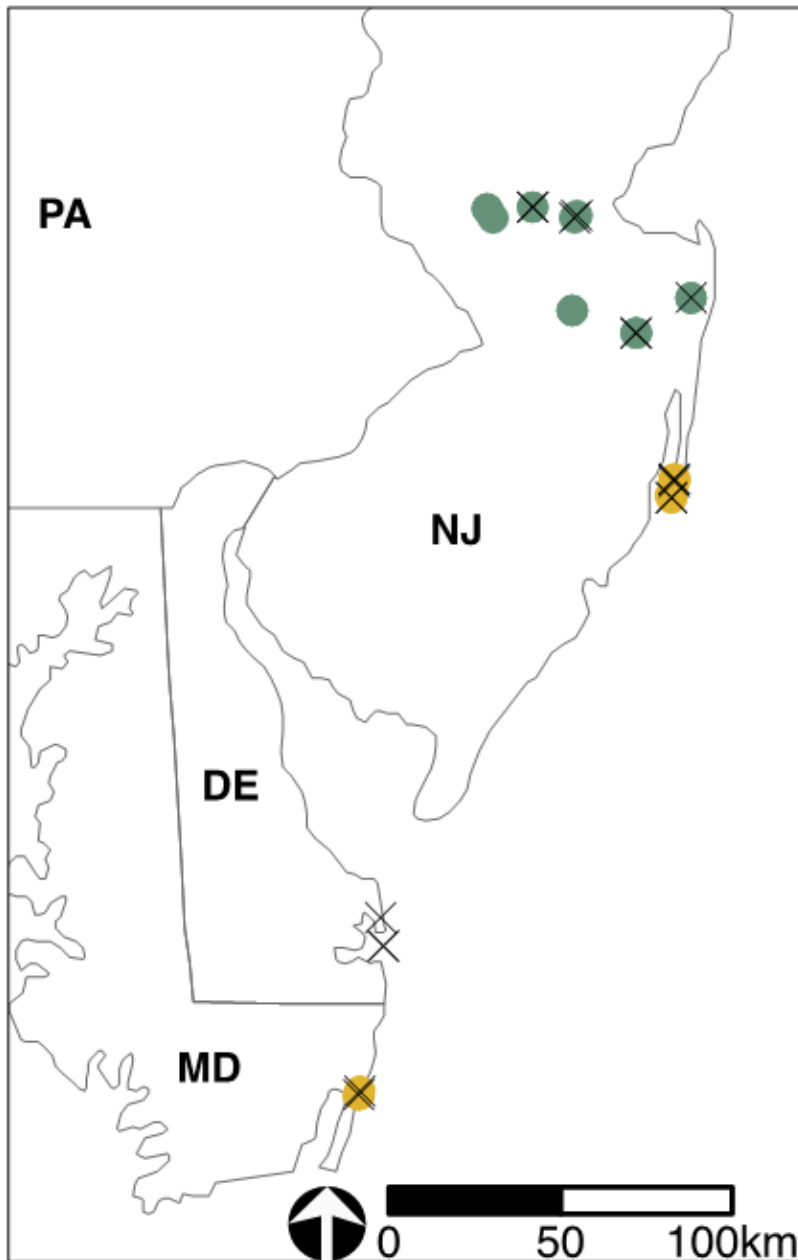


Figure 1

Sampling locations of plant material tested in greenhouse experiments.

X's mark the locations where vine cuttings were sampled from vine patches for testing in the salt spray experiment. Circles represent sampling locations for seeds used for plants for the salt spray, sand burial, and

seedling emergence experiments. The northern-most six locations are inland provenance sampling patches. The lower four locations are the dune provenance sampling patches.



Figure 2

A fabric salt trap measuring salt spray exposure near a small *P. quinquefolia* plant growing on a coastal sand dune.



Figure 3

Plants awaiting salt spray treatment in the greenhouse.

These *P. quinquefolia* vines were planted as seeds, grown, staked, and then tested for foliar salt spray tolerance.



Figure 4

Plants ready for the gradual sand burial experiment.

P. quinquefolia vines were grown in clear plastic pots with some exposed to gradual sand burial treatments and others unburied as control treatments.



Figure 5

The seedling emergence experiment.

a) *P. quinquefolia* seedling emerging from grow mix treatment in a plastic tray.

b) Seedlings emerging from sand in the fabric grow bags planting treatment.

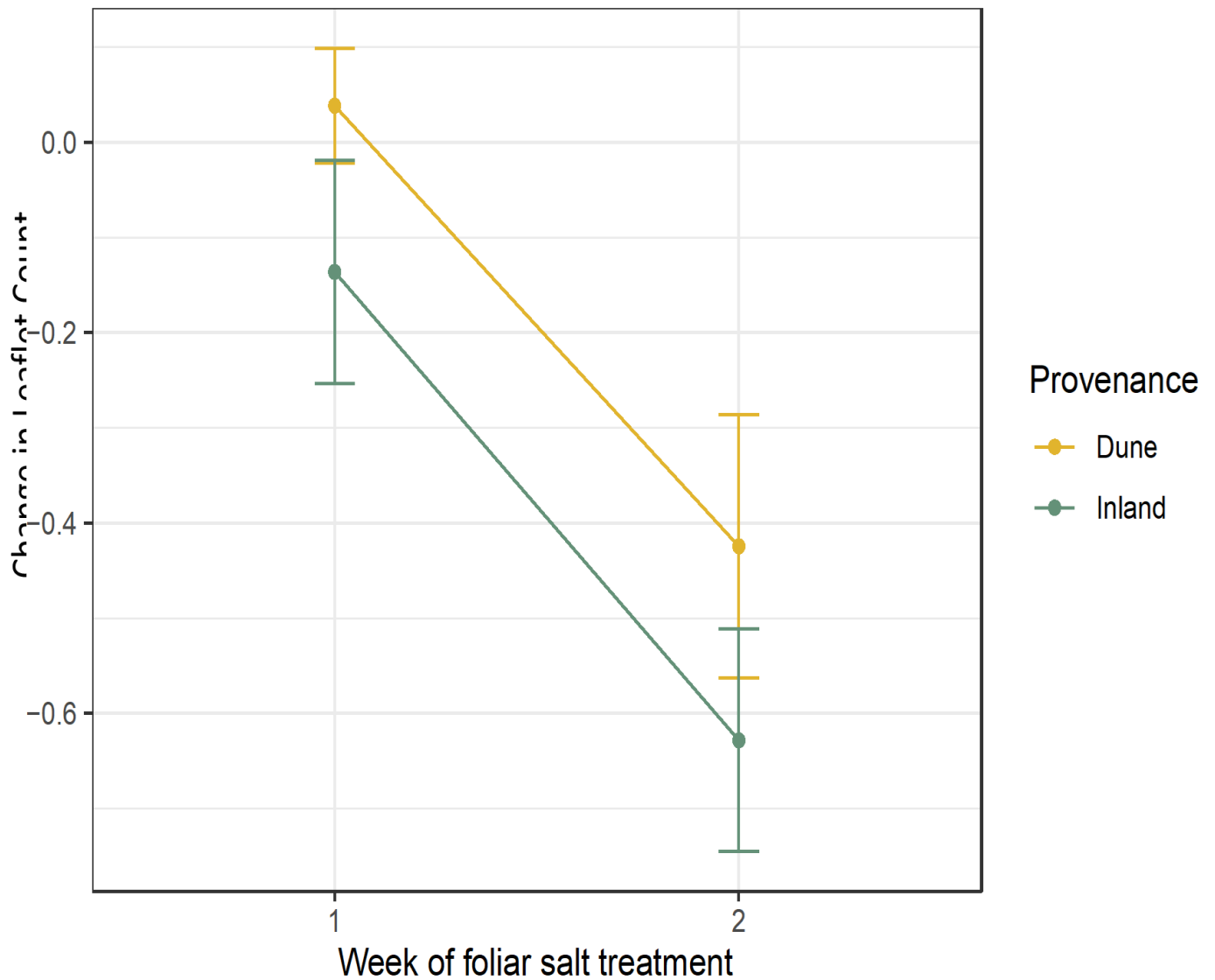


Figure 6

Response of vine cuttings to two weeks of foliar salt treatment.

Each line is the mean Leaflet Relative Change (LRC) for *P. quinquefolia* plants potted from vine cuttings sampled from dune (top line) or inland (lower line) environments. Zero on the y-axis indicates no change and -1.00 represents all leaves necrotic. Error bars represent 95% confidence intervals around the mean. Provenance had a significant impact on change in leaflets at both one and two weeks of salt spray treatment.

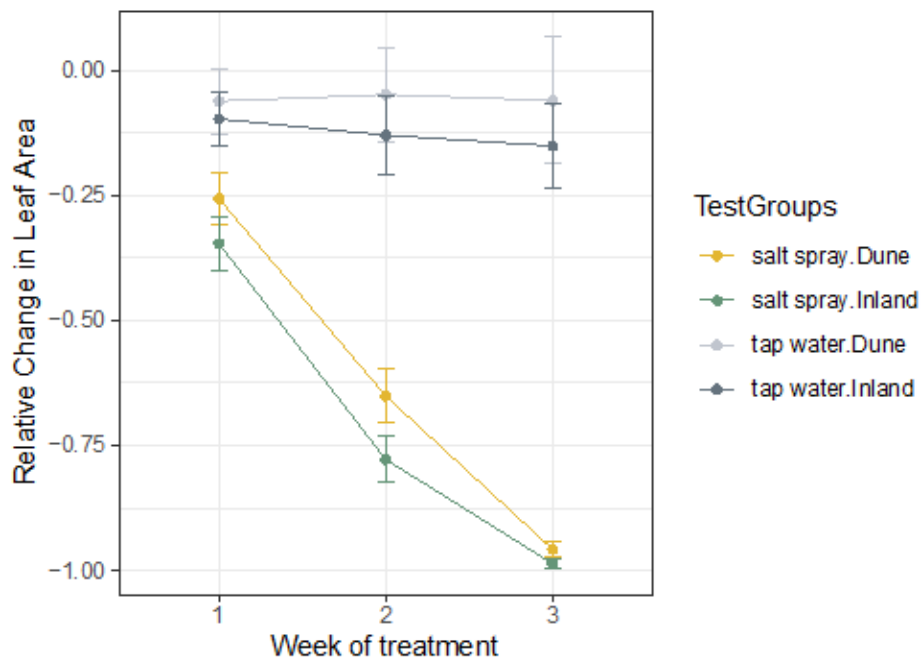


Figure 7

Response of seed grown plants to three weeks of foliar salt spray.

Salt spray had a negative impact on Leaf Area Estimates (LAE). Zero on the y-axis indicates no change and -1.00 represents all leaves necrotic. By the third week of treatment 70% of all salt treated plants had lost all their leaves. Plant provenance had a significant effect on Relative Change in Leaf Area (RCLA) at one and two weeks of treatment, but no difference was detectable at week three of treatment. Error bars represent 95% confidence intervals around the mean.

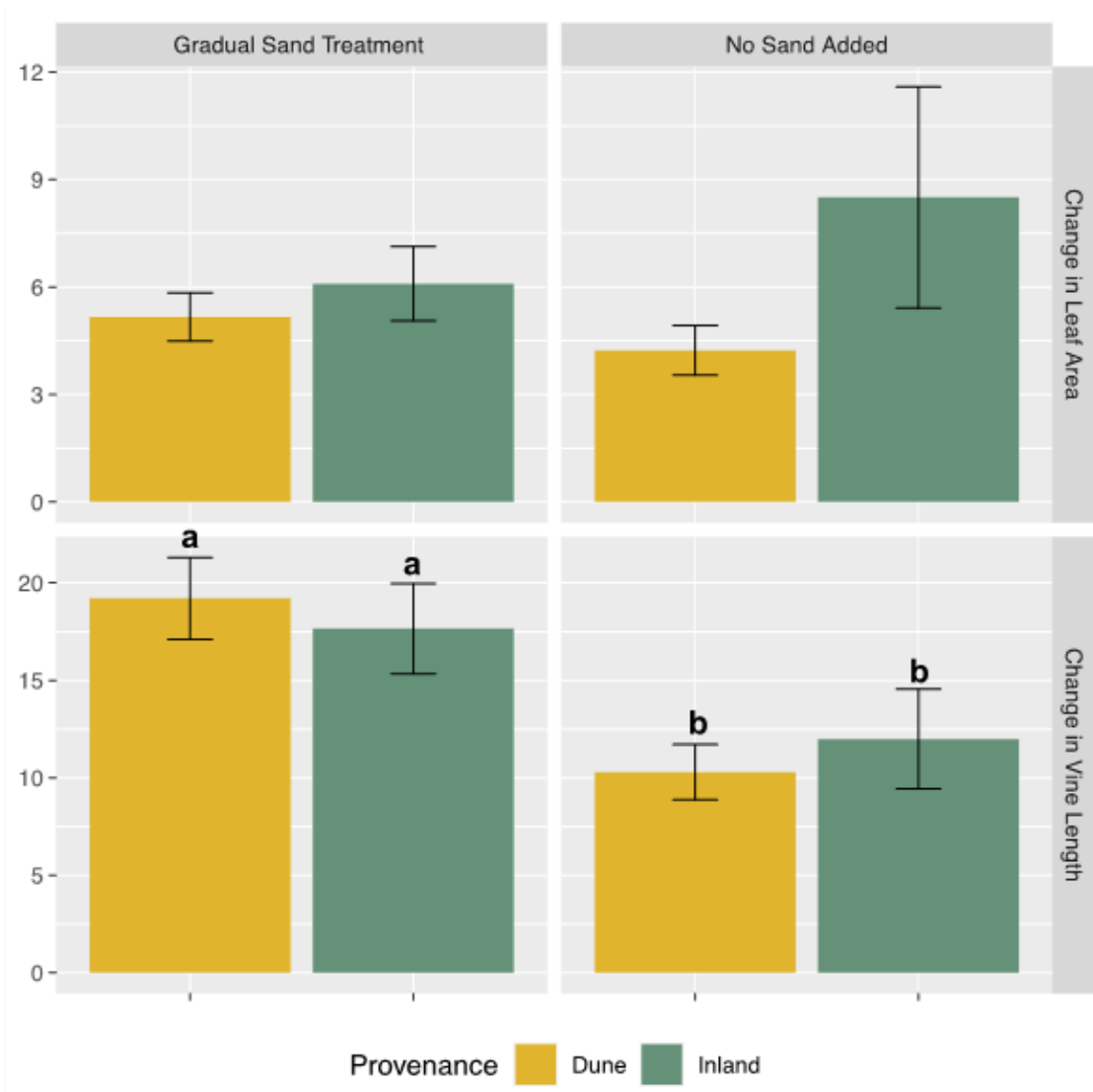


Figure 8

Change of plant growth to gradual sand burial treatment.

Gradual sand burial treatment had no effect on change in leaf area estimates but did increase vine length of buried plants. Bars are the mean relative change in leaf area and vine length of plants grown from seed sampled from dunes and inland vine patches. Error bars represent the 95% confidence levels around each mean. Letters above bars represent significant differences ($p < .05$), as determined with Tukey adjusted post hoc contrast testing, between four test groups: (1) dune plants treated with gradual sand burial; (2) inland plants treated with gradual sand burial; (3) dune plants with no sand added; and (4) inland plants with no sand added. There was no difference between the four test groups in change in leaf area so no letters are added above bars.

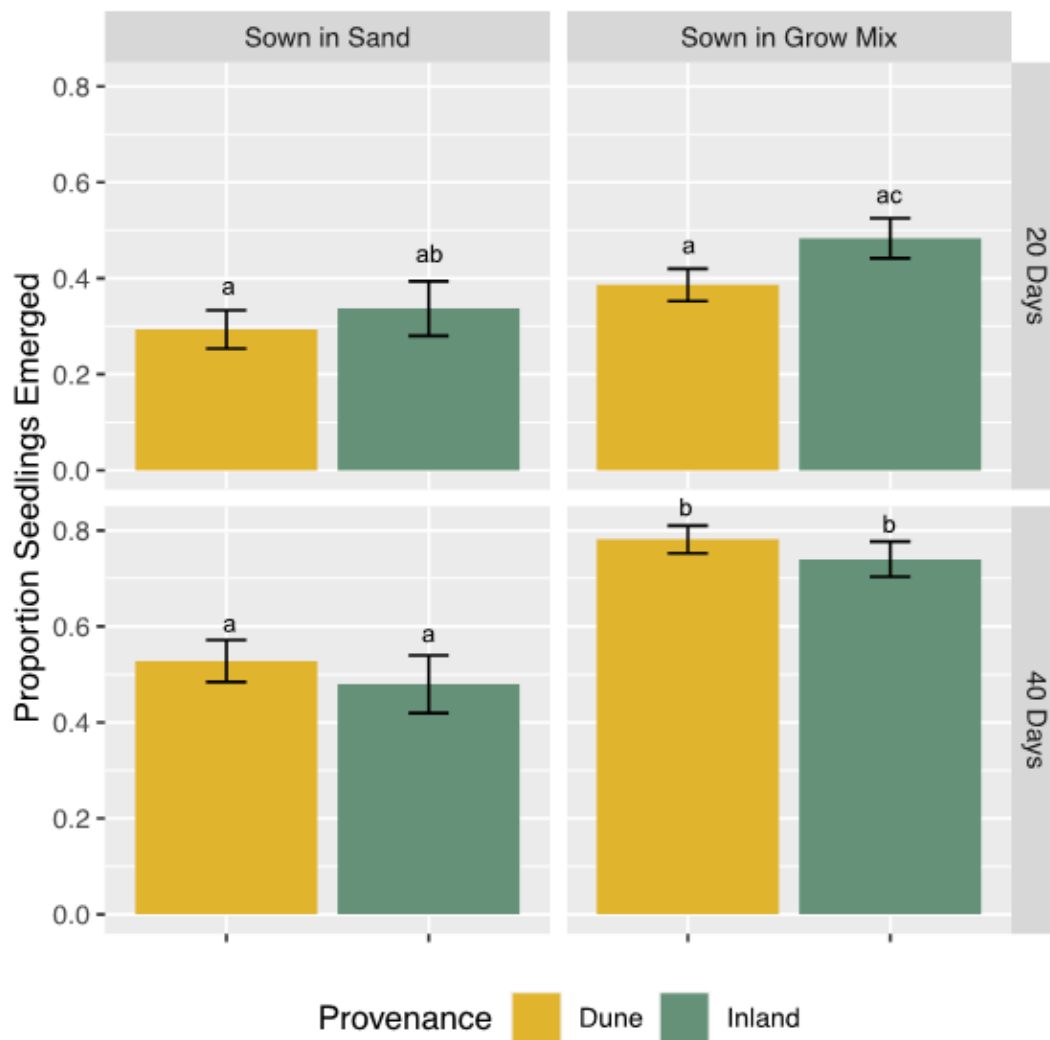


Figure 9

Seedling emergence predicted by growing media and provenance.

In a test of whether seed provenance impacts seedling emergence from two growing media (beach sand and standard grow mix), seedling emergence was recorded 20 and 40 days after the seeds were sown into each media. Provenance (x-axis) had no effect on the mean seedling emergence (y-axis). Error bars represent 95% confidence levels around each mean and letters represent significant differences in pairwise contrasts with Tukey adjusted p values between the four test groups: (1) dune seeds sown in beach sand; (2) inland seeds sown beach sand; (3) dune seeds sown in grow mix; and (4) inland seeds sown in grow mix.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterialSamplinglocationsforexperiments.docx](#)