



Growth of beach-adapted plants in recycled glass sand compared to natural beach sand

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Abstract

Aims The goal of this study was to explore the suitability of recycled glass sand for the growth of beach-adapted plant species given the potential environmental benefits of utilizing glass sand for beach and dune restoration in the face of dwindling natural sand resources.

Methods We grew three species native to US Gulf of Mexico beaches (*Ipomoea imperati* (Vahl) Griseb., *I. pes-caprae* (L.) R.Br., and *Uniola paniculata* (L.)) in three greenhouse experiments in glass sand, beach sand, or mixtures. First, we investigated nutrient and microbial effects by growing each species in pure glass sand, beach sand, and 80%/20% mixtures of glass sand/beach sand. Second, we compared *U. paniculata* growth in glass sand mixed with 100%, 75%, 50%, 25%, or 0% beach sand. These experiments

included fertilizer and microbial sterilization treatments. Third, we investigated soil permeability effects by comparing growth of all species using different grain sizes of glass sand.

Results Overall, plants produced significantly more biomass in beach sand than in glass sand, and the effect was more pronounced with the fertilizer treatment. There were significant effects of substrate mixtures and interactions with fertilizer treatments on *Uniola* biomass. Further, when glass sand grain sizes were manipulated, plant biomass was equal or higher in the coarsest glass sand compared to beach sand.

Conclusions Our results demonstrate that beach-adapted plants can grow in glass sand and suggest that recycled glass sand is a potential resource for ecological restoration with incorporation of soil amendments such as fertilizer and utilization of selected grain sizes.

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Introduction

Sand is an important natural substrate for plant growth in many ecosystems. Sandy beaches and dunes dominate much of the Gulf of Mexico shoreline in the southeastern US, and over 30% of ice-free shorelines around the world (Luijendijk et al. 2018). Beaches are subject to storm surge and rising sea levels, with 24%

of beaches eroding at a rate of at least 0.5 m/yr (Luijendijk et al. 2018). In many areas, major efforts have been undertaken to restore eroding beaches and beach habitats by importing sand from offshore borrow sites such as shoals or from more distant areas when local sources are scarce (Finkl and Khalil 2005; Wildman 2018), a practice known as beach nourishment. However, the use of these external sources of sand is unsustainable (Bird 1990; Liria et al. 2009; Wildman 2018; United Nations Environment Program 2019), and an alternative is to use recycled glass sand, or waste glass which is crushed into fine particles (Babineaux 2012). Recycled glass sand could not only provide a more sustainable source of sand, but also address the issue of glass waste, as discarded glass accounted for 11.11 million metric tons of municipal solid waste in across the US in 2018, of which only 2.78 million metric tons were recycled (US EPA 2023). However, information is lacking on the specific qualities of glass sand that best support beach-adapted plants, especially how glass sand nutrient levels, microbial activity, grain size and various mixtures with natural beach sand affect plant performance.

Glass is made by melting high-quality, chemically pure quartz sand of specific grain size along with soda ash, limestone, and sometimes recycled glass (cullet) (Burkowicz et al. 2020; PFS Aggregates 2021). When glass is pulverized, the resulting recycled glass sand has similar geotechnical properties to beach sand and can be produced to mimic natural sand in its physical and chemical properties (Edge et al. 2003; Kerwin 1997; Makowski et al. 2011). However, the shape and size of particles resulting from the glass crushing process may also affect the permeability and retention of water and nutrients in the substrate (Handreck 1983; Rodriguez 2013; Ouyang et al. 2021; Ma et al. 2022).

Recycled glass from food and beverage containers may contain residual nutrients and microbes, but is unlikely to resemble the microbial community or nutrient profile of beach sand. Indeed, many studies have shown the important role of nutrients and microbes for plant growth in beach sand or sandy soils (Bowen and Rovira 1961; Kachi and Hirose 1983; Koske and Polson 1984; Shin et al. 2007; Khoso et al. 2024). Although a few studies have shown that certain plants and animals can survive and grow in glass sand, including the beach-adapted species *Uniola paniculata* (Breakspere et al. 1980; Makowski et al. 2013; Moller and Leger 1998), it is unclear how differences

in microbial communities and nutrient availability between beach sand and glass sand affect plant growth.

If glass sand is used in beach restoration, it is likely to be intentionally mixed with natural beach sand, as has been reported at Zanzibar Park on the island of Curacao (Makowski et al. 2007), and has been proposed in other beach nourishment projects (Makowski et al. 2007; Monserrate Cid 2018). Aside from ecological reasons, this may be done for aesthetic and commercial reasons (i.e., tourism). If not mixed intentionally, wind and wave action may mix glass sand with the existing beach sand. If nutrients are more available in beach sand than in glass sand, pre-mixing the substrates may improve plant growth. Similarly, if beneficial microbes are present in beach sand, but not in glass sand, pre-mixing could allow those microbes to establish themselves on the glass sand.

To explore the suitability of recycled glass sand as a medium for the growth of beach-adapted plants, we performed a series of three greenhouse experiments using native plants, different experimental substrate mixtures containing recycled glass sand of various grain sizes as well as commercial sand and natural beach sand, and substrate amendments (sterilization, fertilization, and microbial inoculation treatments). After each experiment, subsequent experiments were designed to test hypotheses arising from the results of the preceding experiment. We hypothesized that plants would grow better in beach sand, their natural substrate, than in glass sand, due to the presence of trace nutrients and beneficial microbes in beach sand. We therefore expected that a mixture of beach sand and glass sand would support intermediate growth. We further hypothesized that sterilization of the beach sand would negate some of the growth benefits due to the loss of beneficial microbes, and that fertilizer treatments would reduce the differences in growth between beach sand and glass sand. Following results of initial experiments, we further hypothesized that glass sand grain sizes were affecting permeability of water and oxygen and subsequent plant growth such that using glass sand with larger grain sizes would result in increased growth. Our results confirm that beach-adapted species can grow as well in recycled glass sand as in beach sand, with incorporation of soil amendments such as fertilizer and selection of appropriate grain sizes, and point to the potential for using glass sand to support beach-adapted plant species and its use in beach conservation and restoration.

Methods and materials

Study species

In order to be viable for beach restoration, glass sand must be able to support the growth of beach-adapted plants. In the southeastern Gulf Coast of the US, dune grasses (e.g., *Uniola paniculata*, *Panicum* spp.), and beach morning glories (*Ipomoea* spp.) are abundant on sandy beaches (Craig 1984), and are often planted in coastal restoration and conservation efforts based on their ability to accumulate sand and stabilize sand dunes (Williams 2007).

In our experiments we used three beach-adapted plant species native to the southeastern US Gulf Coast region (see Online Resource Fig. S1): *Ipomoea imperati* (Vahl) Griseb., *Ipomoea pes-caprae* (L.) R.Br. (both Convolvulaceae), and *Uniola paniculata* L. (Poaceae). *Ipomoea imperati* (beach morning glory) and *I. pes-caprae* (railroad vine) are pantropical prostrate perennial vines with stoloniferous growth (Devall 1992; Lonard et al. 2011; Lonard and Judd 1999) whose stolons and adventitious roots capture sand and stabilize coastal beaches and sand dunes. *Uniola paniculata* (sea oats) is an important coastal dune grass in foredune and primary dune environments of the Gulf of Mexico region, and grows exclusively on quartz sand and sand with shell fragments (Lonard et al. 2011). Similar to the morning glories, it stabilizes dunes through expansion of rhizomes, adventitious roots, and erect tillers. All three species are tolerant of drought, salt spray, heat and high sun exposure found in the harsh beach environment (Devall 1992; Lonard et al. 2011; Lonard and Judd 1999). To conduct each of the experiments described below, 5.08 cm (two-inch) plugs of each species were purchased from Green Seasons Nursery (Parrish, Florida, USA).

Plant growth substrates and treatments

Glass Half Full NOLA, a glass recycling company based in New Orleans, Louisiana, USA, collects discarded glass bottles and crushes them into glass particles (glass sand) of multiple grain sizes for a variety of purposes. In our experiments, we used grain size categories of 1.7 mm to 1.1 mm (referred to here as L3), 1.1 mm to 0.4 mm (L4), and <0.4

mm (L5). A 50:50 mixture of L4 and L5 glass sand approximates the grain size distribution of local beach sand (see Online Resource Table S2 for grain size distribution), but we also used larger and smaller grain sizes to bracket typical beach sand. In three greenhouse experiments, we used various substrate combinations including mixtures with natural beach sand collected from vegetated dunes on Dauphin Island, Alabama, USA (30.2497° N, 88.1931° W), a barrier island off of Mobile Bay where previous research occurred (Enwright et al. 2017; Newman et al. 2023). Dauphin Island has a humid subtropical climate (Köppen climate type Cfa; Peel et al. 2007), with mean annual high temperature of 35.0 °C, mean annual low temperature of −2.2 °C, and mean annual precipitation of 148.5 cm (National Oceanic and Atmospheric Administration 2024). The soils of Dauphin Island are sandy, similar to other barrier islands in the region, and are part of the Biloxi Formation (Deramus 1970). Dauphin Island beaches are eroding and are artificially replenished, and all three of the study species grow there. Our experiments were conducted sequentially and incrementally: the results of each experiment informed the design of following experiments. For one treatment in Experiment 1, we added commercial all-purpose sand to natural beach sand to reduce the amount of beach sand from Dauphin Island required as described below.

Given that recycled glass sand is devoid of N and other essential nutrients, we supplied additional nutrients either as a variable treatment (experiments 1 and 2) or uniformly (experiment 3) in the form of Peters Professional 20–20–20 water soluble fertilizer (1.24 g per L water). We also explored how microbes found in beach sand (Corkidi and Rincón 1997; Koske and Polson 1984; van der Putten et al. 1993) can influence plant growth by autoclaving beach sand to eliminate viable microbes. We later controlled for microbial effects using a microbial wash, which was obtained by pouring tap water through beach sand in a sieve and collecting the water draining through the sand. We did not quantify microbial colonization of plant roots here, but rather used plant responses as indicators of their effects. All greenhouse experiments were conducted in Room A of the Tulane University greenhouses, which is unheated and unairconditioned. Wall and roof vents provided ventilation, and evaporative coolers provided cooling.

Geotechnical analysis

We measured four geotechnical properties of all of the substrates used in these experiments: particle size, permeability, porosity, and bulk density.

Particle size distributions were determined by passing sand samples through sieves and weighing the mass of sand captured on each stage.

Permeability describes how easily fluid can pass through a porous medium. For this study, we used the constant head method. A steady state water flow was established through a 1-inch diameter column containing 5–10 inches of glass sand, and then Darcy's law was used to calculate the hydraulic permeability (K) and conductivity (K_c) according to Eqs. 1 and 2, respectively (Whitaker 1986).

$$K = \frac{Q\mu L}{A\Delta P} \quad (1)$$

where K = permeability (m^2), Q = volumetric flow rate (m^3/s), μ = dynamic viscosity ($\text{Pa}\cdot\text{s}$), L = length of filter media (m), A = area of tube (m^2), and ΔP = pressure difference (Pa).

$$K_c = \frac{VL}{AHt} \quad (2)$$

where K_c = hydraulic conductivity (m/s), V = volume of water (m^3), L = length of the filter media (m), A = area of tube (m^2), H = water head (m), and t = time (s).

Porosity describes the void spaces in the media and was calculated from the particle density (ρ_p) and the bulk densities (ρ_b) of the beach and glass sand samples.

The particle density was measured using the displacement method. A known mass of glass sand was added to a known volume of water in a graduated cylinder. The difference in the volume of water was recorded. The particle density was calculated using Eq. 3, based on Singh (2006):

$$\rho_p = \frac{m_s}{V_d} \quad (3)$$

where ρ_p is the particle density, m_s is the mass of sand, and V_d is the volume of water displaced.

To measure the bulk density, a known mass of sand was poured into a graduated cylinder and the volume

was recorded. The bulk density was calculated using Eq. 4, based on Singh (2006):

$$\rho_b = \frac{m_b}{V_b} \quad (4)$$

where ρ_b is the bulk particle density, m_b is the mass of sand, and V_b is the bulk volume of sand.

The porosity was then calculated using Eq. 5, based on Qiu et al. (2015):

$$\text{Porosity} = 1 - \left(\frac{\rho_b}{\rho_p} \right) \quad (5)$$

Experiment 1 – Growth in glass sand

To test the ability of glass sand to support growth, we planted *I. imperati*, *I. pes-caprae* and *U. paniculata* in four different substrates (see Fig. 1A). We used a “beach sand” substrate as a control, which consisted of 80% commercial play sand and 20% beach sand as a source of microbial inoculum. The second substrate was 100% recycled glass sand consisting of a 50:50 mixture of L4 and L5 grain sizes. These grain sizes were chosen to approximate the grain size distribution of beach sand (see Online Resource Table S2), based on our assumption that beach-adapted plants would grow best in substrate that mimics their natural substrate. A third substrate (glass sand mixture) consisted of 80% L4/L5 glass sand, and 20% beach sand in order to test for effects of introducing nutrients and microbial communities from the natural beach sand. The fourth substrate (glass sand sterile mixture) was the same as the third substrate, but the beach sand was autoclaved to eliminate potential microbial effects. To differentiate between nutrient and other substrate effects, half of the plants in each treatment received biweekly fertilizer applications. We employed a full factorial design across 3 species, 4 substrate mixtures, and 2 fertilizer levels, with 24 replicates, for a total of $3 \times 4 \times 2 \times 24 = 576$ pots (see Fig. 1A).

The four experimental substrate mixtures were prepared over several days using a portable concrete mixer that was thoroughly cleaned between mixing different substrates. Individual components in each substrate were measured by volume, and the resulting mixtures were used to fill 10.16×8.89 cm plastic pots. Plants were obtained as small plugs rooted in potting soil. Before planting in October 2022, we

rinsed potting soil off of the roots, blotted the plants dry, and weighed them to the nearest 0.01 g. Pots were arranged in trays, with 8 of the total 24 plants of the same species, substrate, and fertilization treatment per tray. Three weeks after planting, we replaced any apparently dead plants ($n = 86$). Trays were randomly arranged on benches in a greenhouse, and then randomly rearranged every two weeks following fertilization. To support growth outside of the usual growing season, supplemental light was provided from November to March, from 7 to 10 am and from 4 to 7 pm from 1000 W high-pressure sodium bulbs. All plants were watered every 3–4 days.

After 16 weeks of growth in the greenhouse we harvested all plants in early February 2023. Roots were rinsed clean of substrate, above- and below-ground biomass were separated, and all biomass was dried in a drying oven at 60° C for at least 48 h or until sample weight remained constant. We weighed the above- and below-ground biomass of each plant using a digital balance to the nearest 0.001 g.

Experiment 2 – mixture ratios and sterilization

To improve our understanding of microbial and nutrient effects of glass sand and beach sand as substrates for beach-adapted plants, we grew *U. paniculata* in eight experimental substrates consisting of glass sand (50:50 L4/L5 mix) mixed with 25%, 50%, 75%, or 100% beach sand, either sterilized or unsterilized. A ninth treatment (0% beach sand) consisted of pure glass sand (L4/L5). For each substrate, half of the plants received fertilizer biweekly, and half did not (see Fig. 1B).

Following the same procedure used in experiment 1, *U. paniculata* plugs were rinsed of potting soil, blotted, weighed to the nearest 0.1 g, and planted in March 2023. We planted 20 replicates of *U. paniculata* in each substrate mixture, with half receiving fertilizer. This resulted in 10 replicates in each of 9 substrate mixtures, and 2 fertilizer levels, for a total of $10 \times 9 \times 2 = 180$ pots. Pots were arranged in trays with 10 plants of the same substrate and fertilization treatment per tray, and trays were randomly rearranged every two weeks. All plants were watered every 4–7 days. After 17 weeks of growth, we harvested all plants and processed them as in experiment 1.

During June – September 2023, which overlapped with parts of experiments 2 and 3, the Gulf South region of the US experienced extreme heat, causing hotter conditions inside the greenhouse. As a result, plants exhibited symptoms of heat stress which may have negatively impacted their growth. However, we designed these experiments such that plants growing in all substrates experienced the same temperature, light, and humidity conditions.

Experiment 3 – grain size effects

To test the effects of glass sand grain size on plant growth, based on qualitative observations from the first two experiments, we planted all three species in six different substrates: L3, L3/L4, L4, L4/L5, L5, plus 100% beach sand as a control. The two mixtures (L3/L4 and L4/L5) contained a 50:50 mixture of each grain size. Fifteen replicates of each species were planted in each substrate for a total of 270 pots (90 of each species, see Fig. 1C).

Plants were planted in mid-June 2023 using the same procedure as the first two experiments. Pots were placed in trays, with 10 plants per tray, distributed so that each tray contained a single species, but a mix of treatments. All plants received an initial microbial wash, which was prepared by pouring tap water through beach sand in a sieve and decanting the liquid onto the substrate. Every two weeks, all plants received liquid fertilizer treatments and trays were randomly rearranged. During two censuses, we measured height, leaf or tiller number, meristem number and flower number (for morning glories) to assess plant size. Plants were watered every 2–3 days in response to exceptionally hot temperatures (see Experiment 2). This watering regiment was based on the moisture level of the sand and the apparent wilting of the morning glory leaves. Plants were treated with multiple applications of neem oil to control mealybugs (Pseudococcidae), which infested some *I. imperati* plants and a smaller number of *I. pes-caprae* plants. During a census of growth prior to harvest, *I. imperati* showed signs of stress and wilting following the physical handling and untangling of neighboring plants. Further, the two morning glory species produce stolons that grow horizontally, which sometimes rooted in other pots, potentially reducing the effect of the “home” substrate. We carefully uprooted and moved these stolons from neighboring pots whenever we encountered

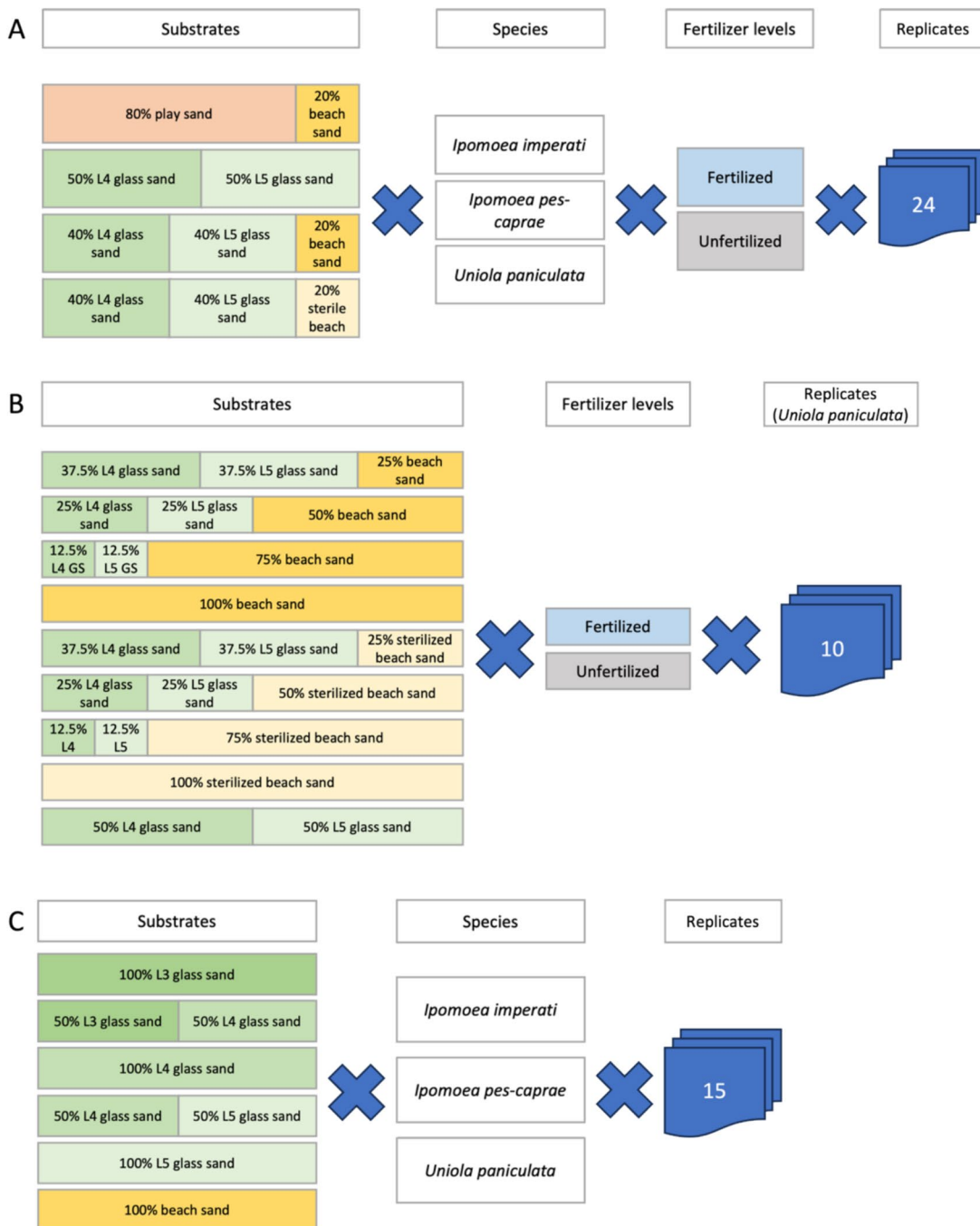


Fig. 1 Diagrams of experimental design for three greenhouse experiments. Bars in the left column of each diagram represent the proportions of different ingredients in each of the substrate treatments. Species names are listed under the heading “Species”, and represent the species included in each of experiments 1 and 3. For experiments 1 and 2, the “Fertilizer Levels” heading lists treatment levels of fertilizer application. The number of replicates for each treatment is listed under the heading “Replicates”. The color of each box corresponds to its

content: shades of green for glass sand, shades of yellow for beach sand, red for play sand, blue for treatments that included fertilizer, and gray for treatments that did not include fertilizer. **A** describes the first experiment, with four substrate treatments, three species, and two fertilization levels. **B** describes the second experiment, with nine substrate levels and two fertilization levels. “GS” refers to glass sand. **C** describes the third experiment, with six substrate levels and three species

them. After 16 weeks of growth, plants were harvested and processed as in the previous experiments.

Statistical analysis

In each experiment, the statistical analyses were similar. For each plant, we obtained the total dry weight biomass and the percent root biomass (below-ground biomass divided by total biomass, times 100) to understand how substrate affected resource allocation to below-ground growth. We fit linear models for dry weight biomass and percent root biomass for each species using the “stats” package in R (R Core Team 2023). In the first two experiments, models of dry weight biomass included linear terms for substrate type, fertilization level and wet weight at planting as a covariate, as well as interaction terms for substrate type by fertilization level and for substrate by fertilization by the covariate at planting. In experiment 3, models of dry weight biomass included only substrate and initial leaf number (for *Ipomoea* spp.) or tiller number (for *U. paniculata*) as a covariate, plus an interaction term. In experiments 1 and 2, percent root biomass models included linear terms for substrate type and fertilization level and an interaction term. In experiment 3, models for percent root biomass included substrate as the only effect. We performed an analysis of variance (ANOVA) on each model to determine the significance of the effect of each variable and interaction. We used the “emmeans” package in R (Lenth 2023) to compute estimated marginal means (EMMs) for each substrate type, conditioned on fertilization level, and to estimate contrasts between substrates, conditioned on fertilization level. We explored transforming the data using a log transformation for dry weight biomass and an arcsine transformation for percent root biomass, but this had little effect on the results of analyses based on the R^2 values of the models, and did not alter the identity of significant factors, so we present results using the untransformed data.

In the third experiment, we also compared the effects on plant biomass of four different geotechnical properties of the substrates (mid-range grain size, permeability, porosity, and bulk density, see Table S2 in Online Resource). This was possible only in the third experiment, where we explored different glass sand mixtures for which we had measured geotechnical properties. For each geotechnical property, we fit a linear model of biomass as a function of that property

and the covariate (initial leaves or tillers) for each plant species, using the “stats” package in R (R Core Team 2023). For comparison, we also fit a linear model using substrate identity and the covariate. We compared the adjusted R^2 value and p-value for the models and the p-values for the geotechnical variable coefficients to determine which variables best predicted growth.

Results

Experiment 1 – growth in glass sand

Substrate and fertilization significantly affected biomass production in all three species (ANOVA: $p < 0.001$ for each species) where plants grown in beach sand had greater biomass on average than those grown in glass sand, regardless of fertilization (EMM: $p \leq 0.027$ for all comparisons). All three species had overall percent root biomass between 30–43%, although with high variability. See Table 1 for details, Online Resource Table S1 for summary statistics and Table S3 for full EMM results.

With fertilization, beach sand outperformed the two sand/glass mixtures as well (EMM: $p < 0.001$ for both comparisons). With no fertilization, growth differences in all three species were less pronounced. In *I. imperati*, growth in beach sand without fertilizer was greater than in any other substrate (EMM: $p \leq 0.021$ for all comparisons). In *I. pes-caprae*, biomass in beach sand without fertilizer was significantly greater than in glass sand without fertilizer (EMM: $p = 0.027$), and in *U. paniculata*, biomass in beach sand without fertilizer was significantly greater than biomass in both glass sand and the unsterilized sand/glass mixture (EMM: $p \leq 0.002$ for both). See Fig. 2 for all biomass comparisons. Across all three species, the main effects, covariate, and all interactions all had a significant effect on total biomass (Table 1).

Substrate had a significant impact on the percent of total biomass represented by roots in *I. pes-caprae* (ANOVA: $p < 0.001$) and *U. paniculata* (ANOVA: $p = 0.001$), and the effect was nearly significant in *I. imperati* (ANOVA: $p = 0.052$). See Fig. 3 for all percent root biomass comparisons. In both morning glory species, when comparing fertilized plants, those grown in beach sand had a lower percent root biomass than those in the other three substrates (EMM: $p \leq 0.001$ for all comparisons), while plants

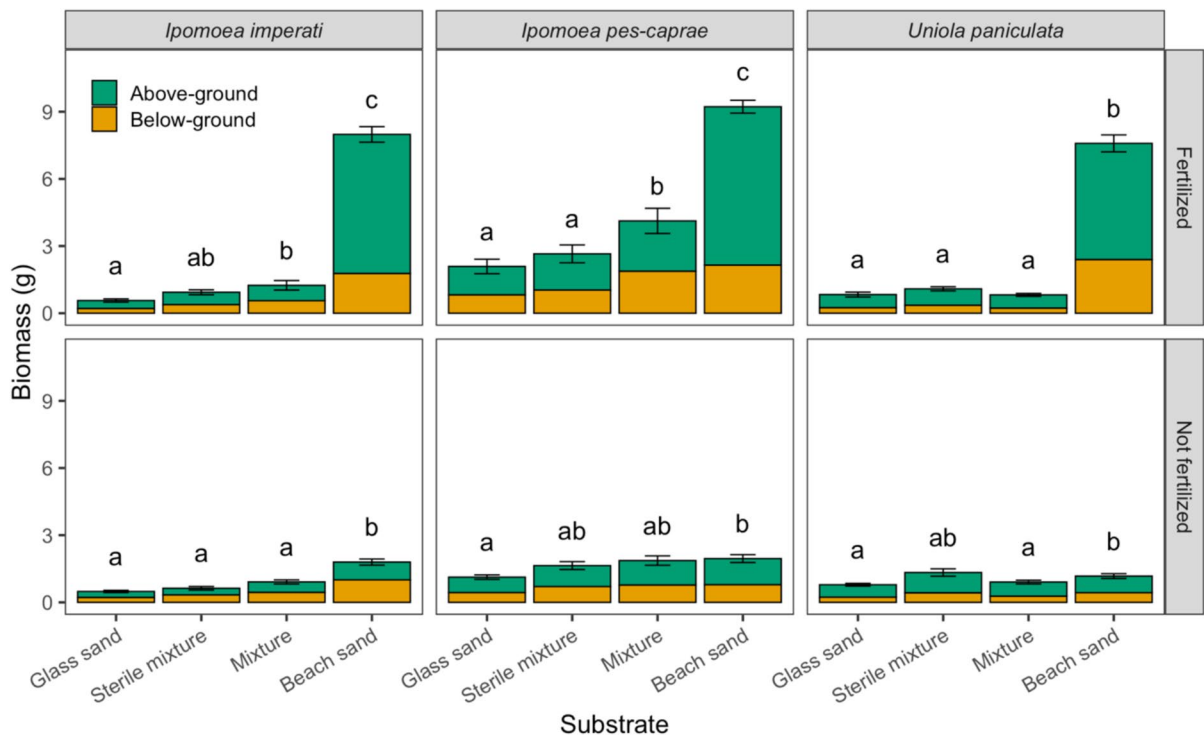


Fig. 2 Bar plots of biomass by species, fertilization, and substrate for experiment 1. Each panel compares mean biomass (in grams) of plants grown in different substrates, with the top row of panels corresponding to plants given fertilizer, the bottom row plants without fertilizer, and each column of panels corresponding to a different species. “Mixture” substrates contained a 50:50 mix of glass sand and beach sand. Bars

are broken down into two sections representing mean above-ground (green) and below-ground biomass (orange) in grams. Bars with different letters differ significantly ($p < 0.05$) based on pairwise comparisons of estimated marginal means within each species and fertilizer treatment. Error bars represent ± 1 standard error

Table 1 Results of ANOVA analysis on models of plant growth in experiment 1. Models of total biomass and models of percent root biomass are summarized. Sources of variance include “substrate”, the specific type of substrate used for planting; “fertilizer”, whether the plant received fertilizer or not; “wet weight”, the weight of the shoot when it was planted

into the experimental substrate; “subs*fert”, an interaction term for substrate and fertilization level, and “subs*fert*ww”, an interaction term for substrate, fertilization level, and starting wet weight. Percent root biomass models did not include terms for wet weight or the interaction of wet weight with other factors, so those rows are left empty

Source	Df	Total biomass models						Percent root biomass models							
		<i>Ipomoea imperati</i>		<i>Ipomoea pes-caprae</i>		<i>Uniola paniculata</i>		<i>Ipomoea imperati</i>		<i>Ipomoea pes-caprae</i>		<i>Uniola paniculata</i>			
		F	P	F	P	F	P	F	P	F	P	F	P		
substrate	3	535.54	< 0.001	106.22	< 0.001	438.2	< 0.001	3	2.62	0.052	11.95	< 0.001	5.61	0.001	
fertilizer	1	375.45	< 0.001	281.96	< 0.001	347.98	< 0.001	1	42.94	< 0.001	15.67	< 0.001	2.15	0.144	
wet weight	1	78.94	< 0.001	112.03	< 0.001	296.95	< 0.001								
subs* fert	3	287.21	< 0.001	76.64	< 0.001	340.97	< 0.001	3	12.12	< 0.001	11.28	< 0.001	1.35	0.260	
subs*fert*ww	7	5.61	< 0.001	2.33	0.027	7.51	< 0.001								
Residuals	176							184							
R ² (adjusted)		0.939		0.832		0.941			0.296		0.291		0.078		

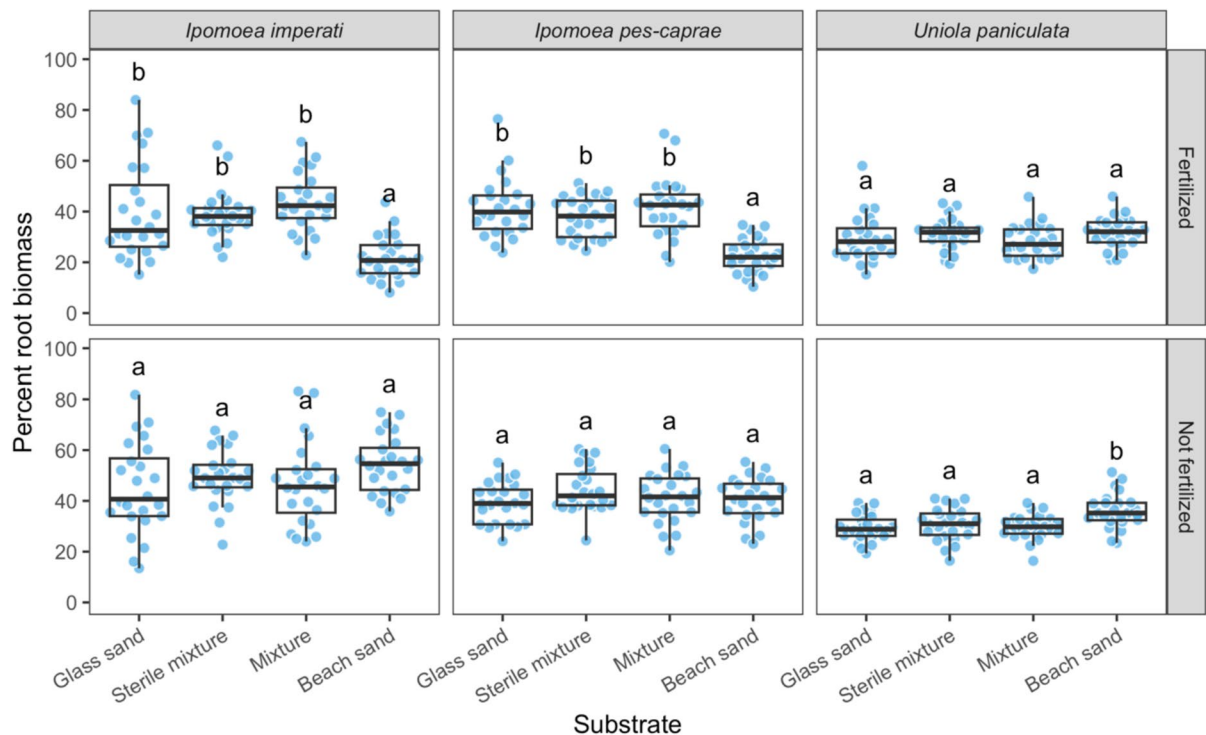


Fig. 3 Boxplots of percent root biomass by species, fertilization, and substrate for experiment 1. Panels compare mean percent root biomass of plants grown in different substrates. “Mixture” substrates contained a 50:50 mix of glass sand and beach sand. The top row of panels displays data from plants

grown with fertilizer, with plants without fertilizer on the bottom. Each column of panels corresponds to a different species. Boxes with different letters differ significantly ($p < 0.05$) based on pairwise comparisons of estimated marginal means within each species and fertilizer treatment

grown without fertilizer showed no significant variation in percent root biomass by substrate (EMM: $p \geq 0.071$ for all comparisons). By contrast, unfertilized *U. paniculata* plants produced a significantly higher percent root biomass in beach sand (EMM $p \leq 0.023$ for all comparisons), while fertilized plants exhibited no statistical differences in percent root biomass across substrates (EMM: $p \geq 0.272$ for all comparisons). Fertilizer had a significant effect on both morning glory species (ANOVA: $p < 0.001$ for both), but not on *U. paniculata* (ANOVA: $p = 0.144$). The substrate-fertilizer interaction was similarly significant only in the morning glories ($p < 0.001$ in both). See Online Resource Table S4 for full EMM results.

Experiment 2 – mixture ratios and sterilization

In the second experiment, analysis of variance revealed that substrate ($p < 0.001$) and starting wet weight ($p < 0.001$) significantly affected final biomass

of *U. paniculata*, as did the interaction of substrate and fertilizer ($p = 0.001$, Table 2). Among plants receiving fertilizer, those in 75% unsterilized beach sand had higher biomass than those in other substrates. However, only a few of these differences (25%, 100% unsterilized beach sand) were significant (EMM: $p \leq 0.022$ for all comparisons, see Fig. 4). In the unfertilized treatments, 25% unsterilized beach sand had significantly less biomass than 100% sterilized (EMM: $p = 0.001$), 75% sterilized (EMM: $p = 0.045$), and 75% unsterilized beach sand (EMM: $p = 0.025$), with the other treatments, including the control, having no statistical differences (EMM: $p \geq 0.108$ for all comparisons). See Fig. 4 for all biomass comparisons and Online Resource Table S5 for full EMM results.

ANOVA results show that substrate had a significant effect on percent root biomass ($p < 0.001$, see Table 2), but fertilizer did not ($p = 0.913$), with no significant interaction effect ($p = 0.234$). While there was no significant overall fertilizer effect,

Table 2 Results of ANOVA analysis on models of *Uniola paniculata* growth in experiment 2. The model of total biomass is summarized first, then the model of percent root biomass. Sources of variance include “substrate”, the specific type of substrate used for planting; “fertilizer”, whether the plant received fertilizer or not; “wet weight”, the weight of the shoot when it was planted into the experimental substrate;

“subs*fert”, an interaction term for substrate and fertilization level, and “subs*fert*ww”, an interaction term for substrate, fertilization level, and starting wet weight. Percent root biomass models did not include terms for wet weight or the interaction of wet weight with other factors, so those rows are left empty

Source	Total biomass models			Percent root biomass models		
	Df	F	P	Df	F	P
substrate	8	4.63	< 0.001	8	5.28	< 0.001
fertilizer	1	0.8	0.372	1	0.01	0.913
wet weight	1	42	< 0.001			
subs*fert	8	3.48	0.001	8	1.33	0.234
subs*fert*ww	17	0.77	0.724			
Residuals	141			159		
R ² (adjusted)		0.328			0.169	

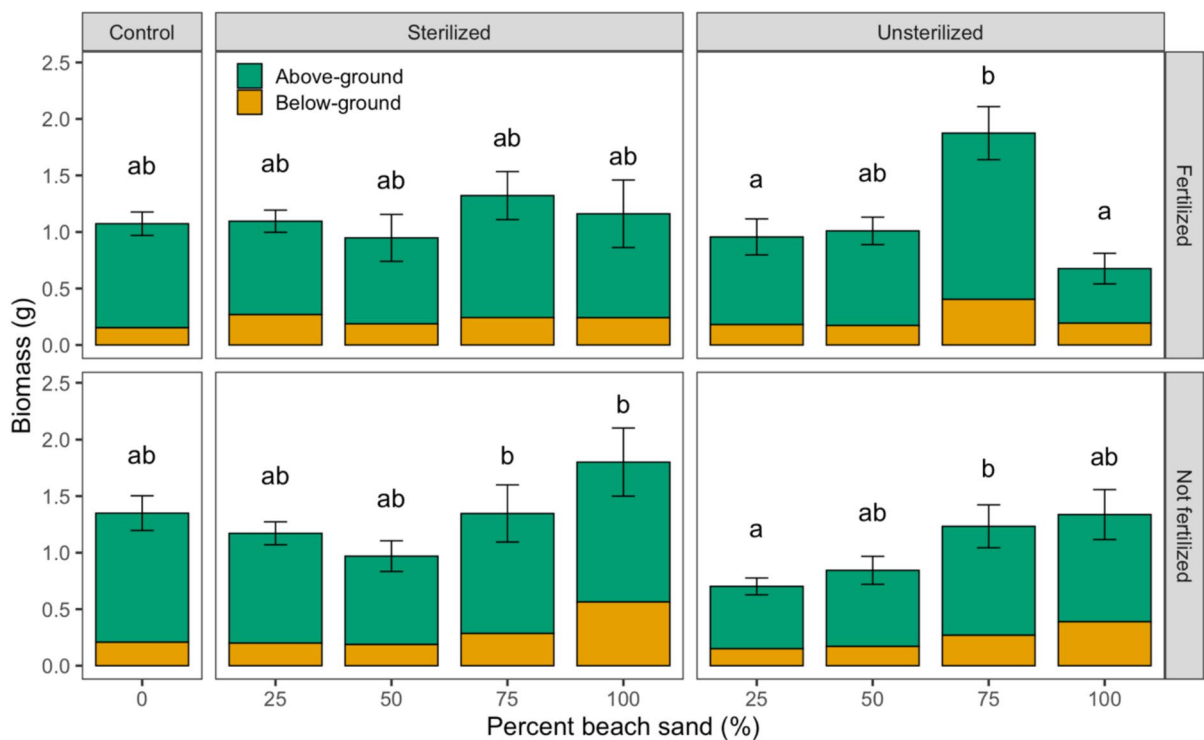


Fig. 4 Bar plots of biomass of *U. paniculata* by fertilization and substrate. Substrates consisted of various mixtures of glass sand and beach sand. The x axis indicates the proportion of the substrate made up of beach sand. Panel labels indicate results for the control (no beach sand), mixes with sterilized beach sand, and mixes with unsterilized beach sand. The top row of panels includes plants that received fertilizer, the bottom row

of panels includes plants that did not receive fertilizer. Bars represent mean total dry weight biomass. The green portion of each bar corresponds to above-ground biomass, and the orange portion corresponds to below-ground biomass. Bars with different letters differ significantly ($p < 0.05$) based on pairwise comparisons of estimated marginal means within each fertilizer treatment. Error bars represent ± 1 standard error

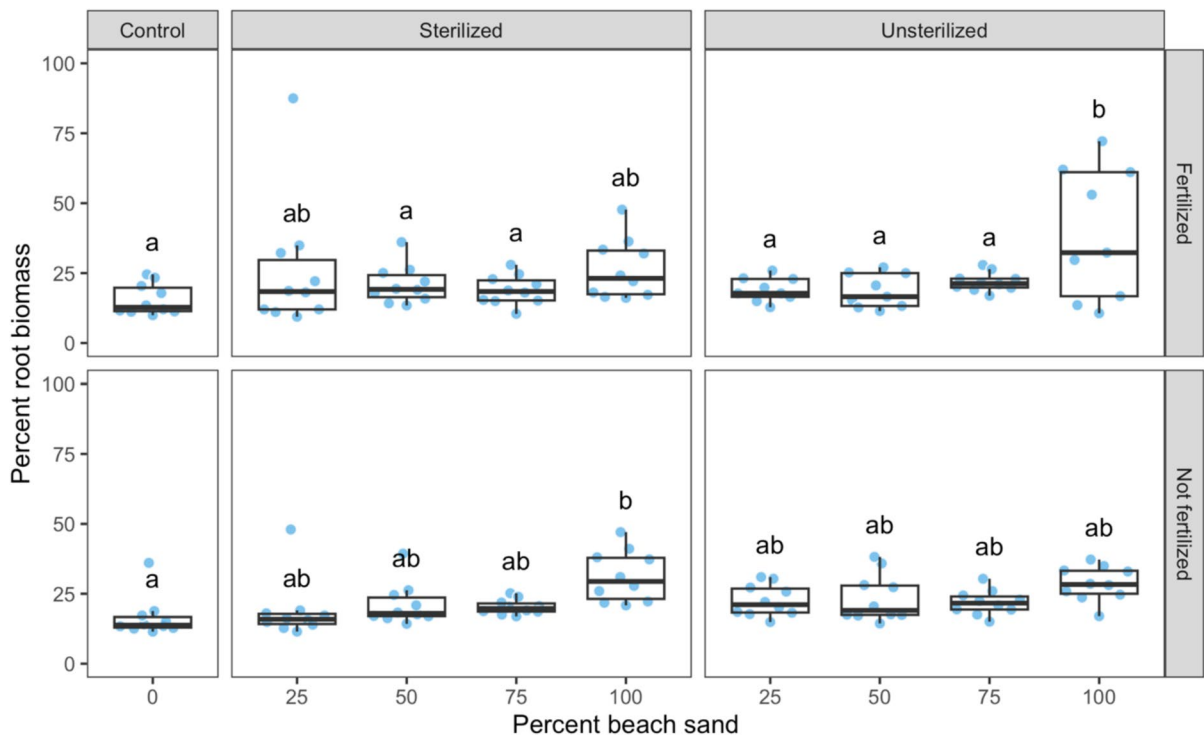


Fig. 5 Boxplots of percent root biomass of *U. paniculata* by fertilization and substrate. Substrates consisted of various mixtures of glass sand and beach sand. The x axis indicates the proportion of the substrate made up of beach sand. Panel labels indicate results for the control (no beach sand), mixes with sterilized beach sand, and mixes with unsterilized beach sand. The top row of panels includes plants that received fertilizer,

the bottom row of panels includes plants that did not receive fertilizer. Boxes represent the median percent root biomass as well as the first and third quartiles. Points in blue correspond to data for individual plants. Boxes with different letters differ significantly ($p < 0.05$) based on pairwise comparisons of estimated marginal means within each fertilizer treatment

among plants that received fertilizer, those in 100% unsterilized beach sand had a higher percent root (EMM: $p \leq 0.008$ for all comparisons) than those in most other treatments (excluding 25% and 100% sterilized beach sand, see Fig. 5). Among non-fertilized plants, those in 100% sterilized beach sand grew more roots than the glass sand control (EMM: $p = 0.032$), while the other treatments did not vary significantly from either of these. See Online Resource Table S6 for full EMM results.

Experiment 3 – grain size

In the third experiment, we analyzed data from 90 plants of each species (270 pots total) where all pots were fertilized equally and received the same microbial wash treatment. Substrate had a highly significant effect on biomass of all three species (ANOVA: $p < 0.001$, see Fig. 6 and Table 3). In general, plants

grew better in glass sand substrates with larger grain sizes, with L3 plants always outperforming L5 and L4/L5 plants (EMM: $p < 0.001$ for all comparisons). Plant biomass in L3 was also greater than in beach sand, although the difference was only significant in *U. paniculata* (EMM: $p = 0.032$). For the two morning glory species, there were no significant differences in biomass production between L4, L3/L4, L3 or beach sand (EMM: $p \geq 0.105$ for all comparisons). Biomass production for all three species was lowest in L5 and next lowest in L4/L5. The initial number of leaves or tillers also had a significant effect on final biomass in *I. imperati* (ANOVA: $p < 0.001$) and *U. paniculata* (ANOVA: $p = 0.005$). There was no significant interaction effect between substrate and the initial size covariate for any of the three species, although in *U. paniculata* the effect was close to being significant ($p = 0.064$). See Online Resource Table S7 for full EMM results.

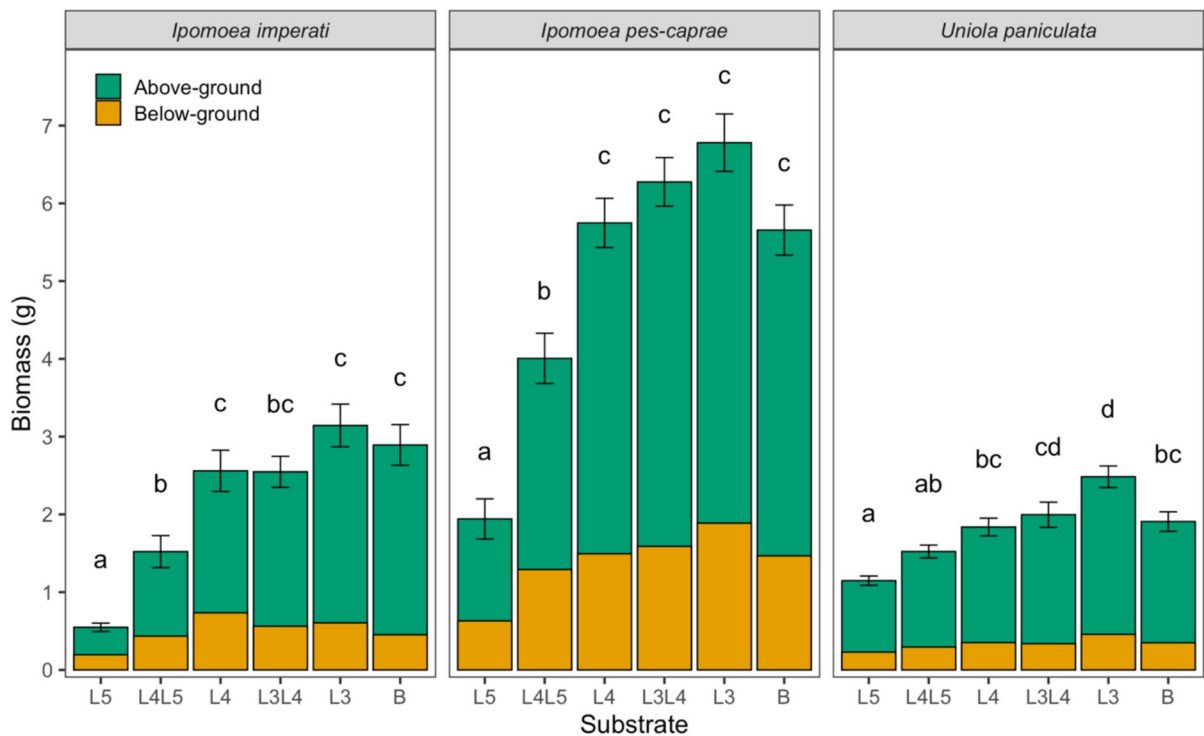


Fig. 6 Bar plots of biomass by species and substrate for experiment 3. Each panel compares mean dry weight biomass (in grams) of plants of a given species grown in different substrates. Substrates are L5, L4/L5, L4, L3/L4, and L3 glass sand, and beach sand (B). Bars are broken down into two

sections representing mean above-ground and below-ground biomass (in grams). Bars with different letters differ significantly ($p < 0.05$) based on pairwise comparisons of estimated marginal means within each species. Error bars represent ± 1 standard error

Table 3 Results of ANOVA analysis on models of plant growth in experiment 3. The model of total biomass is summarized first, then the model of percent root biomass. Sources of variance include “substrate”, the specific type of substrate used for planting; “leaves”, the number of leaves the plant had when

it was planted into the experimental substrate; “subs*leaves”, an interaction term for substrate leaf number. Percent root biomass models did not include terms for leaf number or the interaction of leaf number with other factors, so those rows are left empty

	Total biomass models							Percent root biomass models						
		<i>I. imperati</i>		<i>I. pes-caprae</i>		<i>U. paniculata</i>			<i>I. imperati</i>		<i>I. pes-caprae</i>		<i>U. paniculata</i>	
Source	Df	F	P	F	P	F	P	Df	F	P	F	P	F	P
substrate	5	21.3	< 0.001	30.39	< 0.001	16.82	< 0.001	5	7.43	< 0.001	2.98	0.016	0.75	0.586
leaves	1	12.97	0.001	0.39	0.532	8.45	0.005							
subs*leaves	5	0.36	0.876	0.45	0.809	2.19	0.064							
Residuals	78							84						
R ² (adjusted)		0.553		0.617		0.51			0.265		0.100		− 0.014	

Percent root biomass showed different responses to substrate in different species (Fig. 7). In *I. imperati*, there was a highly significant (ANOVA: $p <$

0.001) effect of substrate, with plants grown in coarser substrates having lower percent root biomass than those grown in finer substrates. Plants of *I.*

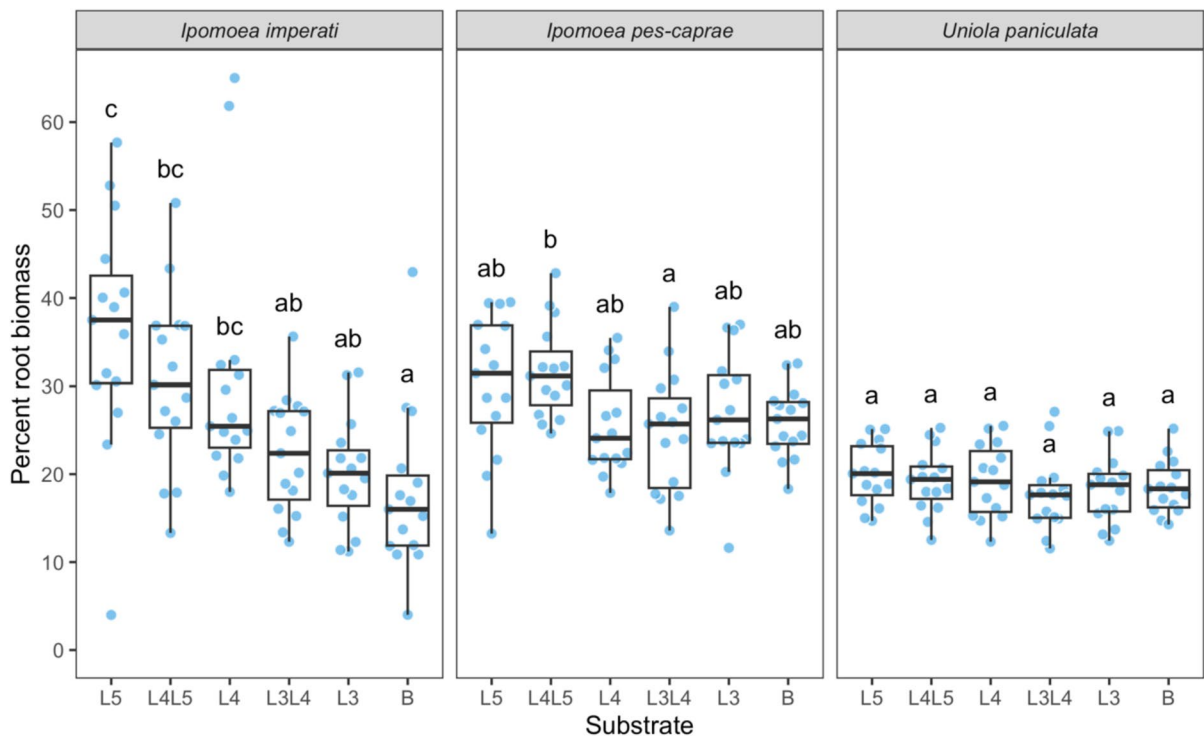


Fig. 7 Boxplots of percent root biomass by species and substrate for experiment 3. Each panel compares mean percent root biomass of plants of a given species grown in different substrates. Substrates are L5, L4/L5, L4, L3/L4, and L3 glass

sand, and beach sand (B). Boxes with different letters differ significantly ($p < 0.05$) based on pairwise comparisons of estimated marginal means within each species

imperati grown in beach sand had the lowest percent root biomass, although the difference between this treatment and the coarsest glass sand was not significant. There was also a significant substrate effect on percent root biomass in *I. pes-caprae* (ANOVA: $p = 0.016$), although the trend was less clear, with L3/L4 having lower percent root biomass than L4/L5 (EMM: $p = 0.038$), and all other pairwise comparisons were nonsignificant (EMM: $p \geq 0.090$ for all comparisons). In *U. paniculata* there was no significant effect of substrate on percent root biomass (ANOVA: $p = 0.586$). See Online Resource Table S8 for full EMM results.

Results of the statistical analysis of the effects of the geotechnical properties of the substrates in experiment 3 on biomass were generally consistent. In all three species, mid-range grain size, permeability, and bulk density (see Online Resource Table S2) were significantly positively correlated with biomass (model and coefficient p -values ≤ 0.002 for all

models, see Table 4). Models that included mid-range grain size explained the most variation in biomass, according to the adjusted R^2 values in Table 4. Porosity was not a significant predictor of biomass according to coefficient p -values (t-test, $p \geq 0.084$ for all comparisons), although the model of *I. imperati* biomass including porosity did achieve overall statistical significance at the 0.05 level (F-test, see Table 4). The “substrate” models, which estimated separate coefficients for each substrate, explained more variation than any of the models based on specific geotechnical properties (Table 4).

Discussion

Our results indicate that plants can grow in glass sand, with coarser grain sizes (L3) being as good or better for plant growth than beach sand, suggesting that recycled glass sand could be used as a plant

Table 4 Statistical analysis of effects of geotechnical properties of substrate on biomass of *Ipomoea imperati*, *I. pes-caprae*, and *Uniola paniculata*. R^2 is the adjusted R-squared value of the linear model. Model p-value is computed with an F-test. Coefficient p-value is the p-value of the coefficient of the given

geotechnical variable in the linear model, computed with a t-test. Coefficient estimate is the coefficient for the given variable in the fit linear model. All models and statistics were computed with the “lm” function from the “stats” package in R (R Core Team 2023)

Species	Geotechnical property	R^2	Model p -value	Coefficient p -value	Coefficient estimate
<i>I. imperati</i>	substrate	0.571	< 0.001	n/a	n/a
	grain size	0.335	< 0.001	< 0.001	1.790
	permeability	0.264	< 0.001	< 0.001	2.653×10^9
	porosity	0.046	0.047	0.084	– 4.751
	bulk density	0.318	< 0.001	< 0.001	4.609
<i>I. pes-caprae</i>	substrate	0.630	< 0.001	n/a	n/a
	grain size	0.478	< 0.001	< 0.001	3.678
	permeability	0.293	< 0.001	< 0.001	4.913×10^9
	porosity	– 0.020	0.887	0.947	– 0.308
	bulk density	0.160	< 0.001	< 0.001	5.706
<i>U. paniculata</i>	substrate	0.474	< 0.001	n/a	n/a
	grain size	0.424	< 0.001	< 0.001	1.010
	permeability	0.365	< 0.001	< 0.001	1.575×10^9
	porosity	0.008	0.259	0.553	– 0.814
	bulk density	0.118	0.002	0.001	1.364

growth substrate and potentially contribute to beach nourishment and restoration.

Nutrient effects

We hypothesized that nutrients present in beach sand would support greater plant growth than in glass sand, and that fertilizer application would negate differences between substrates. Indeed, all three species grew better in unfertilized beach sand than in glass sand. In Experiment 1, fertilizer application did not negate the increased growth effect of beach sand. Instead, fertilization led to greatly enhanced growth in beach sand in all three species, suggesting that plants were more able to access provided nutrients in beach sand, while plants in glass sand did not benefit as much from fertilizer. This is consistent with previous research showing that plants growing in beach sand tend to be limited by nitrogen or phosphorus availability (Kachi and Hirose 1983). The lower percent root biomass in beach sand observed in morning glories treated with fertilizer shows that more resources were allocated to the development of the root system when grown in glass sand as compared to beach sand. This supports the conclusion that nutrient acquisition was less efficient in glass sand compared to beach sand. The impact of

fertilization on *U. paniculata* growth was less clear in Experiment 2, where biomass was greater in a mixture of 75% unsterilized beach sand than in 100% unsterilized beach sand, under fertilizer treatment.

Microbial effects

We hypothesized that beneficial microbes present in natural beach sand would support beach-adapted plant growth, and that the lack of such microbes in glass sand would inhibit growth. In experiment 1, fertilized *I. pes-caprae* grew better in an unsterilized mixture of beach sand and glass sand than in a sterilized mixture, lending some support to this hypothesis. All other species/fertilization level combinations showed no significant difference between sterilized and unsterilized mixtures, although notably, *U. paniculata* growth exhibited a non-significant trend in the opposite direction. In experiment 2, fertilized *U. paniculata* produced the greatest biomass in the 75%, unsterilized mixture. Among unfertilized treatments, *U. paniculata* produced the greatest overall biomass in the 100% sterilized beach sand, and the least biomass in the 25% unsterilized beach sand. The increased growth in 100% sterilized beach sand suggests that microbial pathogens present in natural

beach sand could have negatively impacted *U. paniculata* growth (Bowen and Rovira 1961; van der Putten et al. 1993; David et al. 2016), in contrast to our hypothesis that soil microbes in beach sand would be beneficial to plant growth (Koske and Polson 1984; Shin et al. 2007; Khoso et al. 2024). Previous studies have suggested that grasses, such as *U. paniculata*, are differently affected by pathogens due to their growth patterns and life histories (van der Putten et al. 1993; Clay and van der Putten 1999), which may explain *U. paniculata*'s increased growth in sterilized, unfertilized beach sand. Although we did not elucidate any possible microbial community of commercial play sand, the use of this sand in experiment 1 may have led to differences in the microbial community between these two experiments, which could account for the different effect of sterilized beach sand between *I. pes-caprae* in experiment 1 and *U. paniculata* in experiment 2. The results of both of these experiments suggest a microbial effect, although the direction of the effect varied between plant taxa.

Grain size and substrate permeability effects

We hypothesized that plants would produce more biomass when grown in substrates with larger grain sizes due to its increased permeability. This hypothesis was developed after experiments 1 and 2, in which we observed that pots of all substrates absorbed water slowly after watering, and that the finer L4/L5 glass sand retained water for longer than the beach sand or mixtures did. We also observed that these finer substrates, in the presence of fertilizer, grew a surface layer of algae, with a thicker layer on glass sand pots. These anecdotal observations suggest that the fine glass sand used in this experiment has decreased capacity for drainage, and indeed, geotechnical analysis revealed that the L4/L5 glass sand used in the first two experiments is less permeable to water (and presumably to liquid fertilizer) than beach sand (see Table S2 in the Online Resource).

In experiment 1, plants of all species exhibited the greatest growth in beach sand with fertilizer treatment, and in experiment 2, *U. paniculata* produced more biomass in mixtures containing more beach sand. While we do not have geotechnical data for mixtures of L4/L5 glass sand with beach sand, extrapolating from Table S2 (see Online Resource) suggests that mixtures with more beach sand will have higher

permeability. This suggests that *U. paniculata* produces more biomass in more permeable substrates. We tested our hypothesis that permeability affects growth more directly in experiment 3, which showed that coarser grades of glass sand produced biomass equal to or greater than that produced in beach sand when all pots received regular fertilizer and a microbial wash. This further supports the conclusion that L5 and L4/L5 cause drainage limitations due to the size and shape of those particles, which was also demonstrated by our analysis of geotechnical properties.

Differences in geotechnical properties, particularly permeability, partially explain the observed differences in plant growth between glass sand substrates and natural sand. Through a geotechnical analysis of glass sand and beach sand, we assessed characteristics of grain size, bulk density, permeability, and porosity of the substrates (Table S2 in the Online Resource). Of the materials used, beach sand had the lowest porosity and highest bulk density. Our statistical analysis showed that grain size, permeability, and bulk density were significant predictors of plant growth (Table 4). Linear models of growth versus grain size explained the most variance but cannot account for the growth differences between beach sand and L4/L5, as these two substrates have nearly identical grain sizes. Our observations of water pooling on top of L5 and L4/L5 suggest an important role for permeability, and this is supported by the biomass data: in two of our experiments, plants grew better in beach sand (which is more permeable) than in L4/L5 glass sand. Similarly, in the third experiment, plants grew best in L3, which had the highest permeability among substrates tested (although the growth differences were not always significant). Lower permeability would cause the water to absorb into the substrate and drain from the bottom of the pots more slowly, which could account for the observed pooling of water and algal growth. Increased water retention would reduce oxygen availability in the substrate, affecting nutrient uptake and growth (Ouyang et al. 2021). A previous study found that particles which were spherical and smooth provided less resistance to water flow compared to irregular and rough textured particles (Rodriguez 2013). This suggests that differences in substrate permeability observed here may be related to differences in texture and shape of particles, consistent with previous observations of glass sand by Makowski et al. (2013). However, the greater explanatory power of models based on grain size rather than permeability implies

that permeability is not the only important geotechnical factor and suggests directions for future research into plant growth in glass sand.

Our results are largely consistent with the findings of a previous study in which plants were grown in recycled glass sand. Makowski et al. (2013) planted *U. paniculata* and *Panicum amarum* in an artificial dune constructed from recycled glass sand and found that plant performance was greater than that of plants grown on an adjacent natural sand dune. They suggested that the increased angularity of glass sand relative to natural sand could contribute to greater moisture content of glass sand and better growing conditions. Other studies have demonstrated that adding glass sand to organic soils can promote plant growth, and suggest that the impact on plant growth depends on the grain size (Breakspere et al. 1980) and on the water holding capacity, permeability, and angularity (Moller and Leger 1998) of glass sand. Our results add to this limited body of research with a focus on the effects of varied mixtures of recycled glass sand and natural sand and glass sand particle sizes on plant growth, as well as exploring effects of nutrient addition and microbial inoculation in glass sand mixtures.

Applications in ecological restoration

Our results indicate that glass sand could be a viable replacement for natural sand for beach plant growth. Some advantages of the use of glass sand are that it can be ground to the desired size, it meets contaminant standards, and it has similar physical properties to natural sand (Makowski et al. 2013). Our results highlight some of the differences between glass sand and natural sand and suggest that the coarser mixes of glass sand, such as L3 and L4, are more optimal for plant growth. Based on the biomass production results of experiment 3, the use of L3 glass sand as a growth medium should be of interest in future applications. Although the difference in biomass between the substrates was not significant, future studies could assess the growth of plants over longer periods in a greenhouse or field setting to determine the significance of growth between glass sand and natural sand. Further, future studies could investigate how glass sand substrates affect soil properties such as nutrient levels and water content in natural habitats and how plant physiological processes such as

water potential, stomatal behavior and photosynthetic rate are affected by various substrates and experimental amendments (Kachi and Hirose 1983; Yuan et al. 1993; Shi et al. 2004; Makowski et al. 2013). Future research could also test the effects of glass sand on growth of other beach-adapted species such as *Canavalia rosea* (beach bean), *Helianthus debilis* (dune sunflower) and *Iva imbricata* (beach elder).

Conclusions

Our results from three widespread beach-adapted plant species demonstrate that glass sand can provide an alternative to natural beach sand for plant growth, and suggest that it could be used for beach nourishment using appropriate grain sizes and soil amendments such as fertilizer (see also Makowski et al. 2013). The production of glass sand presents a potential alternative use for waste glass that would otherwise be destined for the landfill. Using recycled glass sand for plant production and for beach and coastal restoration would contribute to a more circular economy and help slow the depletion of natural sand deposits.

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Author contributions All authors were involved in conceptualization, investigation, data curation, validation, and in the drafting, review, and editing of the manuscript. KC and JA provided resources, acquired funding, supervised and administered the project, and designed the methodologies. PR provided software and performed the formal analysis and visualization.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author upon request.

Declarations

Ethics approval No animal subjects were involved in these experiments, so no ethics approval was required.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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