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Growth Characteristics and Anti-Wind Erosion Ability of Three Tropical Foredune Pioneer Species for Sand Dune Stabilization

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Abstract: Rainstorms frequently cause runoff and then the runoff carries large amounts of sediments (sand, clay, and silt) from upstream and deposit them on different landforms (coast, plain, lowland, piedmont, etc.). Afterwards, monsoons and tropical cyclones often induce severe coastal erosion and dust storms in Taiwan. *Ipomoea pes-caprae* (a vine), *Spinifex littoreus* (a grass), and *Vitex rotundifolia* (a shrub) are indigenous foredune pioneer species. These species have the potential to restore coastal dune vegetation by controlling sand erosion and stabilizing sand dunes. However, their growth characteristics, root biomechanical traits, and anti-wind erosion abilities in sand dune environments have not been documented. In this study, the root growth characteristics of these species were examined by careful hand digging. Uprooting test and root tensile test were carried out to measure their mechanical strength, and wind tunnel (6 m × 1 m × 1.3 m, L × W × H) tests were executed to explore the anti-wind erosion ability using one-year-old seedlings. The results of root growth characteristics demonstrate that *I. pes-caprae* is superior to *S. littoreus* and *V. rotundifolia*. Moreover, uprooting resistance of *V. rotundifolia* seedlings (0.074 ± 0.032 kN) was significantly higher than that of *I. pes-caprae* (0.039 ± 0.015 kN) and *S. littoreus* (0.013 ± 0.005 kN). Root tensile strength of *S. littoreus* (16.68 ± 8.88 MPa) and *V. rotundifolia* (16.48 ± 4.37 MPa) were significantly higher than that of *I. pes-caprae* (6.65 ± 2.39 MPa). In addition, wind tunnel tests reveal that sand wind erosion rates for all three species decrease with increasing vegetation cover, but the anti-wind erosion ability of *S. littoreus* seedlings is significantly higher than *I. pes-caprae* and *V. rotundifolia*. Results of root tensile strength and anti-wind erosion ability clearly show that *S. littoreus* is superior to *I. pes-caprae* and *V. rotundifolia*. Taken together, our results suggest that *I. pes-caprae* and *S. littoreus* are beneficial for front line mixed planting, while *V. rotundifolia* is suitable for second line planting in foredune areas. These findings, along with the knowledge on adaption of foredune plants following sand accretion and erosion, provide us critical information for developing the planting strategy of foredune pioneer plants for the sustainable management of coastal foredune ecosystem.

Keywords: anti-wind erosion ability; foredune species; growth characteristics; root biomechanical properties; sand dune stabilization; wind erosion

1. Introduction

Taiwan, a semi-tropical island in East Asia, is highly vulnerable to natural hazards, such as monsoons and tropical cyclones [1]. Torrential rains usually carry large amounts of sandy sediment from upstream and deposit sediments on coastal sand dunes [2]. Strong monsoon winds and tropical cyclones also frequently cause severe coastal erosion disaster and dust storms in Taiwan [3]. Sand dune stabilization and restoration are major challenges in coastal management. Coastal dunes are exposed to harsh environmental conditions, e.g., aridity, high irradiation, high winds, and salt spray [4]. Vegetation can significantly reduce sand erosion [5] and is considered an efficient method for sand dune stabilization [6]. Fore-dune pioneer plants play a significant role in sand dune restoration and coastline protection. Soft intervention technology incorporates natural ecosystems with limited human interference and can achieve self-protection of coastal ecosystems [7]. In Taiwan, *Ipomoea pes-caprae*, *Spinifex littoreus*, and *Vitex rotundifolia* are indigenous fore-dune pioneer species distributed in coastal sand dunes [8–10]. A previous study has reported that these three species have good potential for sand stabilization [11].

Plant growth characteristics and biomechanical properties have significant impacts on coastal sand erosion [12]. Plant root systems were categorized into five kinds, e.g., horizontal (H-), right (R-), vertical and horizontal (VH-), vertical (V-), and massive (M-) type [13]. Mickovski et al. [14] reported that plant uprooting force is strongly influenced by plant traits, and vetiver grass (*Vetiveria zizanioides*) possesses the uprooting force to resist soil erosion. Saifuddin et al. [15] showed that plants with higher root tensile strength have higher uprooting resistance. Lee et al. [16] indicated that tree uprooting force is influenced by some root characteristics, e.g., stem base diameter and biomass. Few studies have been conducted on growth characteristics, root biomechanical properties, and anti-wind erosion ability of *I. pes-caprae*, *S. littoreus*, and *V. rotundifolia*. Kamakura and Furukawa [17] showed that the root system of *I. pes-caprae* belongs to adventitious roots (M-type). Divyasree and Raju [18] reported that *S. littoreus* possesses adventitious roots, and propagates through vegetative stolon formation. He [19] indicated that *V. rotundifolia* develops deep taproot system. Mckovski et al. [14] also demonstrated that vetiver plants with fibrous root system tend to have wider distribution and have a higher uprooting resistance than plants with narrower root system spread. Li et al. [20] showed that due to the taproot system of *Vitex negundo* var. *heterophylla*, root asymmetry lacked a relation with uprooting resistance. However, dune vegetation cover significantly reduces the transport of sand by wind and dune encroachment [21,22]. Udo and Takewaka [23] indicated that vegetation canopy with low height, high density, and flexibility is more effective in reducing wind erosion rate. Meng et al. [24] also demonstrated that vegetation coverage has significant effect on wind erosion. However, growth characteristics, root biomechanical properties, and anti-wind erosion ability of these three species has not been fully explored. The objectives of this research were to (1) examine the growth traits, root biomechanical characteristics, and anti-wind erosion ability of three fore-dune species and (2) analyze the differences among them to use in coastal engineering for sand dune stabilization and vegetation restoration.

2. Materials and Methods

2.1. Seed Collection

Plants of *I. pes-caprae*, *S. littoreus*, and *V. rotundifolia* were chosen from the coastal vegetation situated at Houlong Village, Miaoli County, Taiwan (120°48'53.18"E, 24°40'4.18"N) in August 2017. Capsules of *I. pes-caprae*, caryopses of *S. littoreus*, and drupes of *V. rotundifolia* were gathered in October 2017 and dried in steel trays. Seeds were separated, cleaned, and kept in polythene zip-lock bags at ambient conditions.

2.2. Seedling Raising

In December 2017, seeds were cleaned, surface sterilized with 15% sodium hypochlorite solution, and then germinated in sterilized planting materials [16]. After attaining a mean height of 5.4 ± 1.2 cm in March 2018, seedlings were transplanted into two kinds of wooden boxes (i.e., tall boxes, 30 cm \times 30 cm \times 100 cm, L \times W \times H and short boxes, 50 cm \times 40 cm \times 30 cm, L \times W \times H). Prior to transplanting, the boxes were filled with sand dune soils gathered from the same coastal area. The sandy soil consists of 91.0% sand, 7.2% silt, and 1.8% gravel. The sandy soil from a sand dune used in this research had poor soil fertility. The chemical properties of the sandy soil were pH 8.32, EC 0.04 ds m^{-1} , total N 0.02%, available P 15.0 mg kg^{-1} , available K 31.0 mg kg^{-1} , calcium 801 mg kg^{-1} , and organic matter 0.18 mg kg^{-1} . For growth characteristics and root mechanical features investigation, 24 seedlings were transplanted to 24 tall boxes separately. For wind tunnel test, 50 plants of each species were planted to 180 short boxes, respectively. All boxes with seedlings were randomly placed in nursery under ambient conditions and watered daily. Boxes were rotated every week to minimize the shading effect. Concurrently, the azimuth of box was unchanged.

2.3. Growth Characteristics Observation

One year after transplanting, 12 seedlings of each species were randomly selected for growth characteristics investigations. Seedling height (H) and stem base diameter (SBD) were measured. Roots were excavated and flushed with water to expose the intact root system. Root growth characteristics were examined and recorded. Root system images were taken for further investigation of growth characteristics. Root growth characteristics were estimated using WinRHIZO Pro root analysis software [25], while root volume was calculated using the water displacement method to prevent miscalculation [26]. Root and shoot were dried in an oven at 75°C for 72 h to evaluate dry biomass. Root growth characteristics were calculated [27,28]. Meanwhile, single root samples were selected for subsequent tensile tests.

2.4. Uprooting Test

Twelve plants of each species were randomly chosen for uprooting determinations. The sandy soil has a mean dry weight of 16.5 kN m^{-3} and water content of $14.2 \pm 2.3\%$ measured at 30-cm below soil surface using soil moisture meter [16]. Before each test, plant height and stem base diameter were measured. The stem was cut off from 20 cm above the stem base by pruning shear, wrapped with polytetrafluoroethylene sealing strip, and then attached to the uprooting device using steel clamps. The uprooting test was performed using an uprooting apparatus [16]. The ultimate uprooting force (F_{ult} , N) was registered for statistical analysis.

2.5. Root Tensile Test

After excavation, single root samples were classified into three diameter classes (0–1, 1–2, and 2–5), except for *S. littoreus*, which had only two diameter classes (0–1 and 1–2). Root samples were prepared and preserved [29]. Only undamaged root segments were used. One hundred and twenty root segments of each species were tested, and tensile tests were conducted within 24 h of collection. Root tensile strength tests were conducted using a tensile testing device [16]. For each species, 120 root samples from the middle section were tested: 73 root samples of *I. pes-caprae*, 75 root samples of *S. littoreus*, and 100 root samples of *Vitex rotundifolia*. The following formula was used to calculate root tensile strength (T_{si} , MPa) [30–32]:

$$T_{si} = \frac{4F_{ult}}{\pi D_i^2} \quad (1)$$

where F_{ult} is the ultimate force at breakage (N), and D_i is the average root diameter (mm) measured at three points.

In addition, the relation between root tensile strength (T_s) and diameter (D) was calculated using a power law equation [33]:

$$T_s = \alpha \cdot D^{-\beta} \quad (2)$$

where α and β are empirical constants contingent upon species.

2.6. Wind Tunnel Test

Wind tunnel tests were completed to assess wind erosion rates of different vegetation cover of the three species. The wind tunnel was established using a steel frame covered by polycarbonate sheets (600 cm × 100 cm × 130 cm, L×W×H). The wind generator consisted of a blower fan with a rigid plastic pipe, set in front of the wind tunnel [34]. In addition, an acrylic horizontal sand collector (80 cm × 30 cm × 25 cm, L × W × H) was put behind the box to collect wind-blown sand [35]. A pilot study showed that by adjusting the distances between blower fan and soil surface of the box from 160 cm to 80 cm, the wind speeds reached $6.3 \pm 0.3 \text{ m s}^{-1}$ and $10.8 \pm 0.4 \text{ m s}^{-1}$, respectively. Wind erosion tests were carried out under these two conditions. The temperature in tunnel was $27 \pm 5 \text{ }^\circ\text{C}$ during the day, with 50%–65% relative humidity. At the beginning of the wind erosion tests (April 2019), a sand moisture content of $1.5 \pm 0.3\%$ in the upper 10 cm of each box was monitored using soil moisture meter to avoid wet sand effect on sand erosion rate [36,37]. Vegetation cover images of cover of each box were taken, recorded, and analyzed with ImageJ software (US NIH, Bethesda, MD, USA). Seedlings in the boxes were carefully thinned to vegetation covers of 20%, 40%, 60%, and 80%, respectively. Boxes without plantings served as control. Subsequently, boxes with different vegetation covers of the three species were arranged in the wind tunnel separately, and artificial wind applied automatically for 5 min. The tests consisted of three species, five vegetation covers, two wind speeds, and six replicates. The wind speed was monitored and recorded at the leeward side of the soil surface. Wind-blown sands were collected and measured for further analysis.

2.7. Statistical Data Analysis

Variations in growth characteristics, root biomechanical properties, and anti-wind erosion rates among species were analyzed using one-way ANOVA and significant differences in means compared using Tukey's HSD post hoc tests ($p < 0.05$). Descriptive statistics of plant height, total root length, and root surface area were normalized, analyzed by multicollinearity tests, and multiple linear regression analyses using SPSS Version 22.0 (IBM, Armonk, NY). Multiple regression analyses were performed using Multiple Regression Analysis in SPSS to investigate relationships between uprooting resistance and root growth characteristics among species. Microsoft Excel Regression analysis (Excel 2013, Microsoft, Redmond, WA) was used to investigate the relations between root tensile resistance, tensile strength, and root diameter among species.

3. Results

In coastal sand dunes of Taiwan, *I. pes-caprae*, *S. littoreus*, and *V. rotundifolia* are native foredune pioneer species well-adapted to the harsh environmental conditions. *I. pes-caprae* is a procumbent perennial sand-fixing vine, with sprawling vines and leathery leaves, distributed along sandy seashores. *S. littoreus* is a perennial grass, with hard culm and sharp pointed blades, distributed in littoral sand dunes. *V. rotundifolia* is a prostrate shrub, with pubescent leaves, distributed in coastal sandy areas (Figure 1).



Figure 1. Morphology of *I. pes-caprae* (a), *S. littoreus* (b), and *V. rotundifolia* (c) plants. Photo taken by M.-J. Lee and K.-H. Chao in August 2018.

3.1. Growth Characteristics

Experimental testing showed the boxes had sufficient space for root growth during the study period. Analytical data showed that growth characteristics of seedlings varied greatly among species, except the number of root tips (Table 1). On average, *I. pes-caprae* plants (198.1 ± 38.3 cm) were significantly taller than *V. rotundifolia* (145.6 ± 31.5 cm) and *S. littoreus* (103.4 ± 34.1 cm). Stem base diameter was largest for *I. pes-caprae* (9.1 ± 0.6 mm) and *S. littoreus* (7.4 ± 1.6 mm) and smallest for *V. rotundifolia* (6.1 ± 2.5 mm). Total root length was significantly longer for *I. pes-caprae* (790 ± 135.3 cm) than for *V. rotundifolia* (557.5 ± 292.5 cm) and *S. littoreus* (441.5 ± 150.3 cm). Root biomass of *I. pes-caprae* (9.6 ± 3.8 g) was significantly higher than that of *V. rotundifolia* (3.9 ± 1.8 g) and *S. littoreus* (0.5 ± 0.3 g). In addition, shoot biomass of *I. pes-caprae* (46.5 ± 9.9 g) was significantly higher than that of *V. rotundifolia* (27.4 ± 9.2 g) and *S. littoreus* (9.6 ± 4.8 g). Overall, *I. pes-caprae* seedlings produced significantly more shoot and root growth than *V. rotundifolia* and *S. littoreus* seedlings.

Table 1. Variation in growth characteristics for the seedlings of the three foredune species.

Growth Characteristics	<i>I. pes-caprae</i>	<i>S. littoreus</i>	<i>V. rotundifolia</i>	One-Way ANOVA (F)
H (cm)	198.1 ± 38.3^a	103.4 ± 34.1^c	145.6 ± 31.5^b	11.187 ***
SBD (mm)	9.1 ± 0.6^a	7.4 ± 1.6^a	6.1 ± 2.5^b	4.366 *
RT	1206 ± 451.6^a	734.7 ± 229.2^a	1163.8 ± 816.8^a	1.326
TRL (cm)	790 ± 135.3^a	441.5 ± 150.3^b	557.5 ± 292.5^b	4.482 *
RB (g)	9.6 ± 3.8^a	0.5 ± 0.3^c	3.9 ± 1.8^b	11.993 ***
SB (g)	46.5 ± 9.9^a	9.6 ± 4.8^c	27.4 ± 9.2^b	6.306 **
RD (kg m^{-3})	0.18 ± 0.07^a	0.02 ± 0.01^b	0.07 ± 0.05^b	12.256 ***
RLD (km m^{-3})	0.15 ± 0.02^a	0.08 ± 0.03^b	0.1 ± 0.05^b	4.515 *
RSA (cm^2)	696.5 ± 194.16^a	187.43 ± 87.78^b	304.71 ± 230.72^b	12.969 ***
RTD (g cm^{-3})	0.19 ± 0.06^a	0.07 ± 0.03^b	0.26 ± 0.11^a	9.750 **
RV (cm^3)	57.67 ± 34.25^a	6.85 ± 4.51^b	11.79 ± 9.27^b	11.047 ***
SRL (m g^{-1})	0.89 ± 0.23^c	11.41 ± 4.78^a	3.98 ± 0.91^b	13.777 ***

Means \pm SDs for growth characteristics of the three species. Growth characteristics include plant height (H), stem base diameter (SBD), number of root tips (RT), total root length (TRL), root biomass (RB), shoot biomass (SB), root density (RD), root length density (RLD), total root surface area (RSA), root tissue density (RTD), root volume (RV), and specific root length (SRL). Different superscript letters within the same row signify significant differences (Tukey's HSD post hoc testing) among species. N = 12. Significance level * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

I. pes-caprae and *V. rotundifolia* seedlings grew longer root systems than *S. littoreus* seedlings (Figure 2). The root systems for *I. pes-caprae* and *S. littoreus* were classified as M- (massive) type as defined by Yen [13]. However, the root system of *V. rotundifolia* was classified as VH- (vertical horizontal) type. *I. pes-caprae*, a vine plant, developed deep lateral roots up to 90 cm deep in sand (Figure 2a). *S. littoreus*, a grass, grew its fibrous roots up to 50 cm deep in sand (Figure 2b). *V. rotundifolia*, a shrub, grew its tap root up to 60 cm deep in sand (Figure 2c).

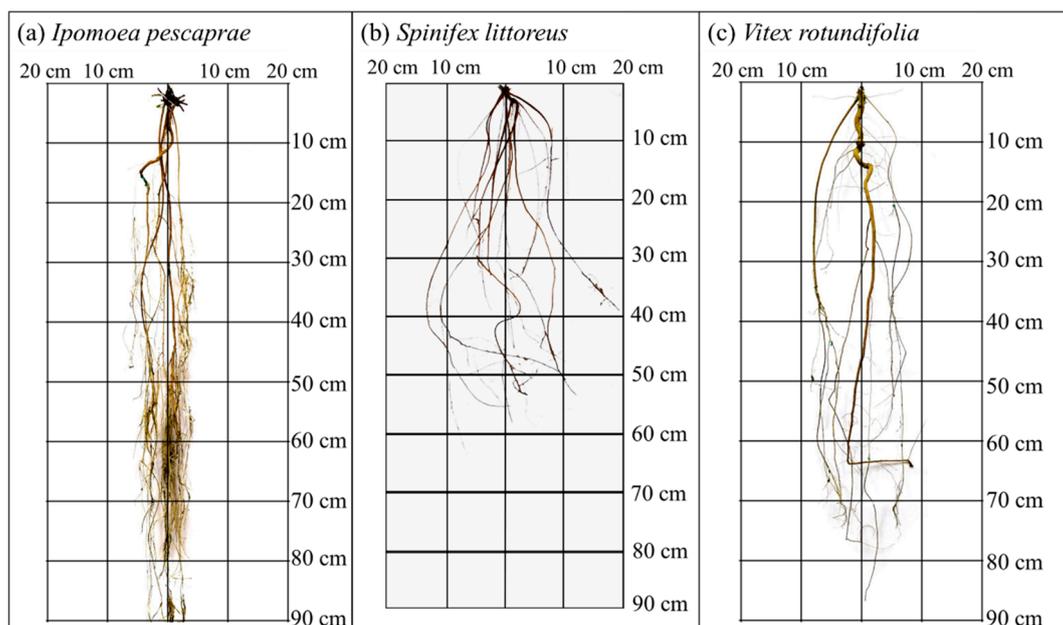


Figure 2. Representative root system morphology of one-year-old *I. pes-caprae* (a), *S. littoreus* (b), and *V. rotundifolia* (c) seedlings.

Root growth characteristics were significantly different among species (Table 1). Mean root density of *I. pes-caprae* ($0.18 \pm 0.07 \text{ kg m}^{-3}$) was significantly higher than that of *V. rotundifolia* ($0.07 \pm 0.05 \text{ kg m}^{-3}$) and *S. littoreus* ($0.02 \pm 0.01 \text{ kg m}^{-3}$). Root length density of *I. pes-caprae* ($0.15 \pm 0.02 \text{ km m}^{-3}$) was significantly higher than that of *V. rotundifolia* ($0.1 \pm 0.05 \text{ km m}^{-3}$) and *S. littoreus* ($0.08 \pm 0.03 \text{ km m}^{-3}$). Root surface area of *I. pes-caprae* ($696.5 \pm 194.16 \text{ cm}^2$) was significantly higher than that of *V. rotundifolia* ($304.71 \pm 230.72 \text{ cm}^2$) and *S. littoreus* ($187.43 \pm 87.78 \text{ cm}^2$). Root tissue density of *V. rotundifolia* ($0.26 \pm 0.11 \text{ g cm}^{-3}$) and *I. pes-caprae* ($0.19 \pm 0.06 \text{ g cm}^{-3}$) were significantly higher than that of *S. littoreus* ($0.07 \pm 0.03 \text{ g cm}^{-3}$). Root volume of *I. pes-caprae* ($57.67 \pm 34.25 \text{ cm}^3$) was significantly higher than that of *V. rotundifolia* ($11.79 \pm 9.27 \text{ cm}^3$) and *S. littoreus* ($6.85 \pm 4.51 \text{ cm}^3$). However, specific root length of *S. littoreus* ($11.41 \pm 4.78 \text{ m g}^{-1}$) was significantly higher than that of *V. rotundifolia* ($3.98 \pm 0.91 \text{ m g}^{-1}$) and *I. pes-caprae* ($0.89 \pm 0.23 \text{ m g}^{-1}$). Altogether, the root growth characteristics of *I. pes-caprae* were significantly higher than that of *V. rotundifolia* and *S. littoreus*.

3.2. Plant Uprooting Resistance

Uprooting resistance increased with displacement up to the highest point and dropped as the roots broke (Figure 3). The ultimate uprooting resistance of *V. rotundifolia* ($0.074 \pm 0.032 \text{ kN}$) was almost double that of *I. pes-caprae* ($0.039 \pm 0.015 \text{ kN}$) and almost six times that of *S. littoreus* ($0.013 \pm 0.005 \text{ kN}$). Regression analysis results showed a positive relation between the ultimate uprooting resistance and some growth characteristics, those being plant height, total root length, and root surface area. Linear regressions of uprooting resistance (U_r) and plant height (H) for *I. pes-caprae*, *S. littoreus*, and *V. rotundifolia* seedlings are: $U_r = -0.0004H + 0.1124$ ($R^2 = 0.8755$, $p = 0.006$), $U_r = 0.0001H - 0.0009$ ($R^2 = 0.8057$, $p = 0.015$) and $U_r = 0.0014H - 0.1307$ ($R^2 = 0.7128$, $p = 0.034$), respectively. Linear regressions of uprooting resistance (U_r) and total root length (TRL) for *I. pes-caprae*, *S. littoreus*, and *V. rotundifolia* seedlings are: $U_r = 0.0001\text{TRL} - 0.048$ ($R^2 = 0.9522$, $p = 0.001$), $U_r = 0.00003\text{TRL} - 0.0016$ ($R^2 = 0.9418$, $p = 0.001$) and $U_r = 0.0002\text{TRL} - 0.0225$ ($R^2 = 0.8892$, $p = 0.002$), respectively. Furthermore, linear regressions of uprooting resistance (U_r) and root surface area (RSA) for *I. pes-caprae*, *S. littoreus*, and *V. rotundifolia* seedlings are: $U_r = 0.000007\text{RSA} - 0.0092$ ($R^2 = 0.771$, $p = 0.021$), $U_r = 0.000006\text{RSA} + 0.0029$ ($R^2 = 0.864$, $p = 0.007$) and $U_r = -0.0003\text{RSA} + 0.000001$ ($R^2 = 0.947$, $p = 0.00004$), respectively.

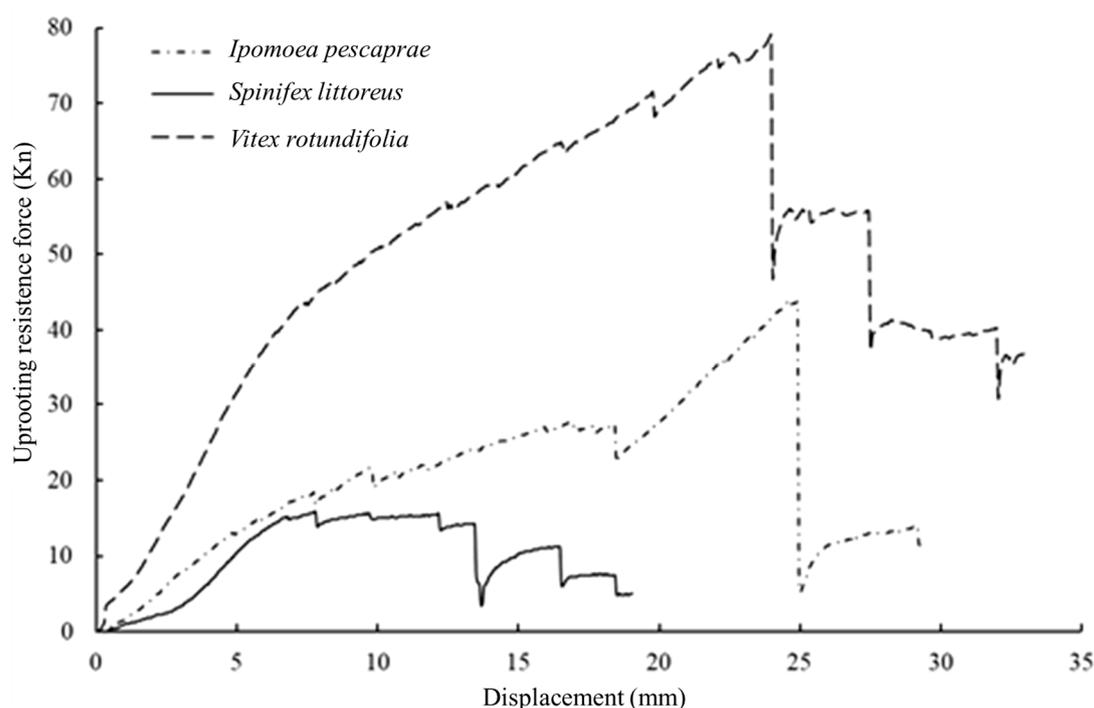


Figure 3. Typical uprooting resistance–displacement curves for the three foredune species.

Multicollinearity tests demonstrated that variance inflation factors (VIF) of plant height and root surface area for *I. pes-caprae*, *S. littoreus*, and *V. rotundifolia* were 3.151, 2.690, and 3.167, respectively, signifying no collinearity between plant height and root surface area. The derived multiple linear regression equations are:

For *I. pes-caprae* seedlings, $U_r = -0.263H + 0.026RSA - 72.846$ ($R^2 = 0.910^*$, $r = 0.954$, $p = 0.027$, VIF = 3.151).

For *S. littoreus* seedlings, $U_r = 0.066H + 0.035RSA - 0.12$ ($R^2 = 0.934^*$, $r = 0.966$, $p = 0.017$, VIF = 2.690).

For *V. rotundifolia* seedlings, $U_r = 0.115H + 0.212RSA - 7.757$ ($R^2 = 0.990^{***}$, $r = 0.995$, $p = 0.001$, VIF = 3.167).

where U_r is uprooting resistance (N), H is plant height, RSA is root surface area, and p is significance level. Taken together, the uprooting resistance of *V. rotundifolia* is significantly higher than that of *I. pes-caprae* and *S. littoreus*.

3.3. Root Tensile Strength

One-way analysis of variance of the data demonstrated that root diameter, tensile resistance, and tensile strength varied greatly among species. The average root diameter was largest for *V. rotundifolia* (1.73 ± 1.02 mm) and *I. pes-caprae* (1.61 ± 0.79 mm) and lowest for *S. littoreus* (0.76 ± 0.39 mm). The mean root tensile resistance force of *V. rotundifolia* (42.69 ± 39.38 N) was significantly higher than that of *I. pes-caprae* (13.68 ± 11.3 N) and *S. littoreus* (6.24 ± 3.86 N). The mean root tensile strength was highest for *S. littoreus* (16.68 ± 8.88 MPa) and *V. rotundifolia* (16.48 ± 4.37 MPa) and lowest for *I. pes-caprae* (6.65 ± 2.39 MPa) (Table 2). In addition, mean root tensile strength differed significantly for root diameter classes among species (Table 3). For 0–1 and 1–2 cm diameter classes, mean root tensile strength of *V. rotundifolia* and *S. littoreus* were at least double that of *I. pes-caprae*. Moreover, root tensile resistance decreased with decreasing root diameter following a power law function (Figure 4). However, root tensile strength increased with decreasing root diameter following a power law curve (Figure 5). Altogether, the tensile strengths within roots of *V. rotundifolia* and *S. littoreus* were significantly higher than that of *I. pes-caprae*.

Table 2. Variation in root parameters for the three foredune species.

Root Parameters	<i>I. pes-caprae</i>	<i>S. littoreus</i>	<i>V. rotundifolia</i>	One-Way ANOVA (F)
Root diameter (mm)	1.61 ± 0.79 ^a	0.76 ± 0.39 ^b	1.73 ± 1.02 ^a	34.270 ^{***}
Tensile resistance force (N)	13.68 ± 11.3 ^b	6.24 ± 3.86 ^c	42.69 ± 39.38 ^a	49.477 ^{***}
Tensile strength (MPa)	6.65 ± 2.39 ^b	16.68 ± 8.88 ^a	16.48 ± 4.37 ^a	76.298 ^{***}

Means ± SDs for root parameters of the three species. Different superscript letters within the same row signify significant differences (Tukey's HSD post hoc testing) among species. Significance level: *** $p < 0.001$.

Table 3. Variation in root tensile strength for the three foredune species.

Root Diameter (mm)	Tensile Strength (MPa)		
	<i>I. pes-caprae</i>	<i>S. littoreus</i>	<i>V. rotundifolia</i>
0–1	9.38 ± 0.49 ^b	19.76 ± 1.17 ^a	20.53 ± 0.98 ^a
1–2	6.18 ± 0.27 ^c	8.76 ± 0.48 ^b	16.37 ± 0.36 ^a
2–5	4.97 ± 0.18 ^b	–	13.37 ± 0.4 ^a

Means ± SDs for root tensile strength of different root diameter classes. Different superscript letters within the same row signify significant differences (Tukey's HSD post hoc testing) among species. Significance level $p < 0.001$.

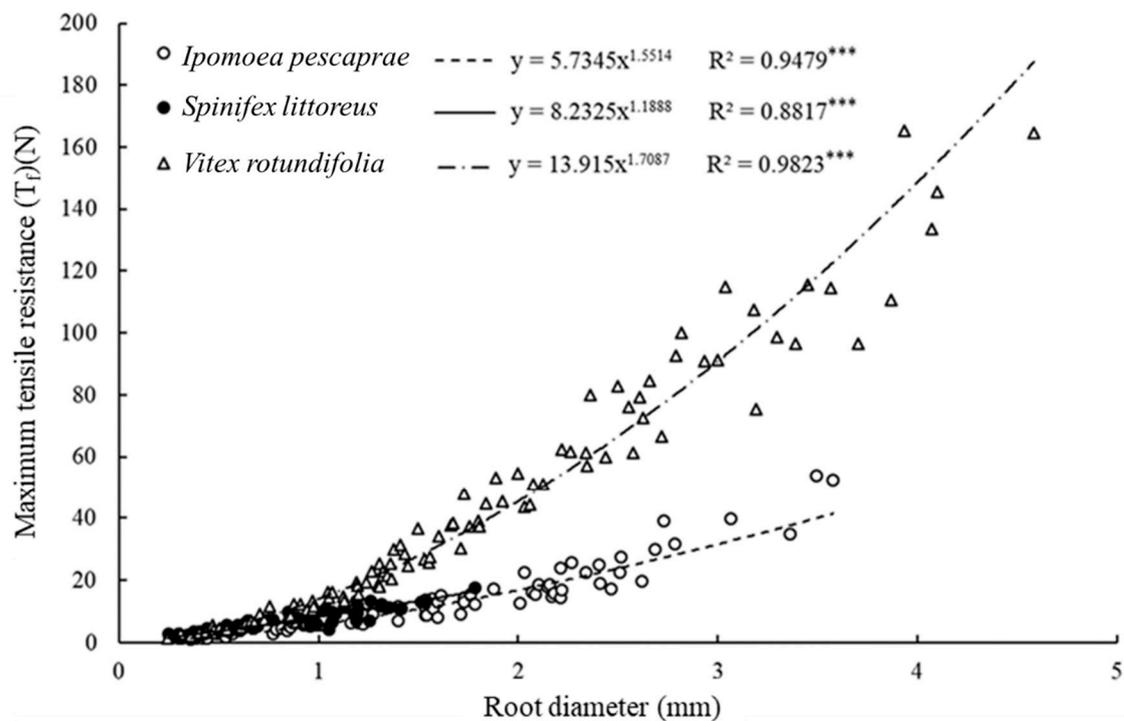


Figure 4. Root tensile force–root diameter relations for the three foredune species. Significance level *** $p < 0.001$.

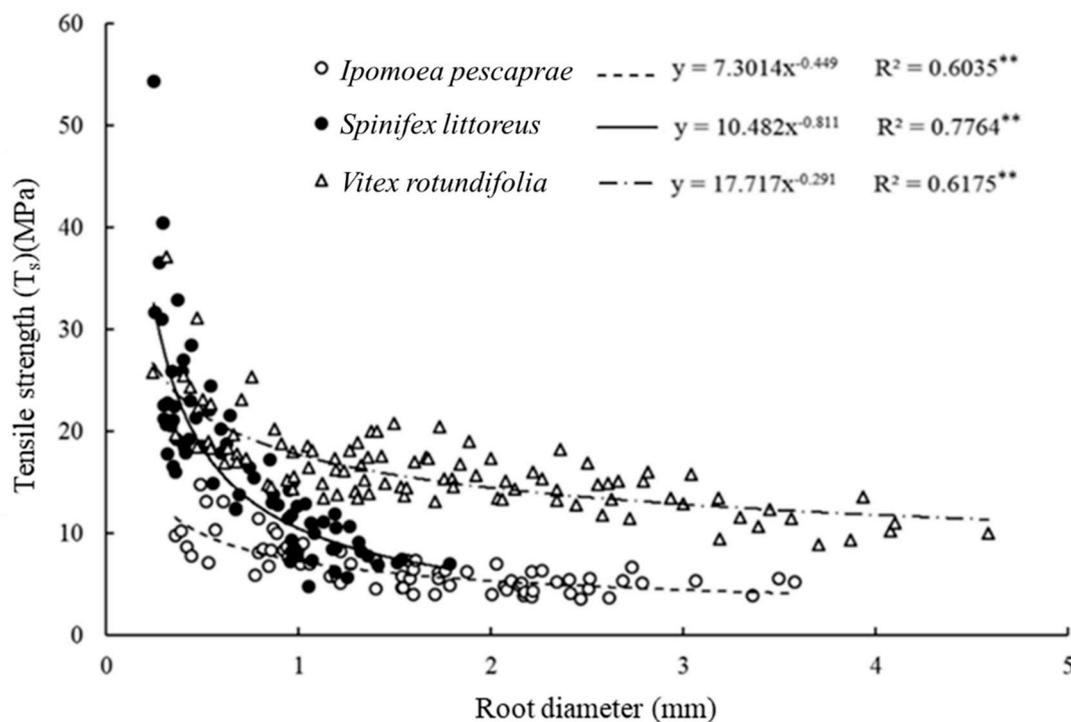


Figure 5. Root tensile strength–root diameter relations for the three foredune species. Significance level ** $p < 0.01$.

3.4. Anti-wind Erosion Ability

Experimental results showed that leeward soil surface wind speed was highly varied among the three species. Mean leeward soil surface wind speed differed significantly among species under windward wind speeds of 6.3 ± 0.3 and $10.8 \pm 0.4 \text{ m s}^{-1}$. At a windward wind speed of $6.3 \pm 0.3 \text{ m s}^{-1}$ and vegetation cover of 20%, the mean leeward soil surface wind speeds of *V. rotundifolia* ($4.63 \pm 0.11 \text{ m s}^{-1}$) and *I. pes-caprae* ($4.58 \pm 0.07 \text{ m s}^{-1}$) were at least 10% higher than that of *S. littoreus* ($4.15 \pm 0.07 \text{ m s}^{-1}$), whereas under the vegetation cover of 60%, leeward soil surface wind speeds of *V. rotundifolia* ($3.63 \pm 0.05 \text{ m s}^{-1}$) and *I. pes-caprae* ($3.24 \pm 0.09 \text{ m s}^{-1}$) were at least 28% higher than that of *S. littoreus* ($2.52 \pm 0.05 \text{ m s}^{-1}$) (Table 4). On the other hand, under windward wind speed of $10.8 \pm 0.4 \text{ m s}^{-1}$ and vegetation cover of 60%, leeward soil surface wind speeds of *I. pes-caprae* ($4.89 \pm 0.12 \text{ m s}^{-1}$) and *V. rotundifolia* ($4.82 \pm 0.06 \text{ m s}^{-1}$) were at least 20% higher than that of *S. littoreus* ($3.86 \pm 0.09 \text{ m s}^{-1}$) (Table 5). Furthermore, wind erosion rates were significantly different among species. At a windward wind speed of $6.3 \pm 0.3 \text{ m s}^{-1}$ and vegetation cover of 20%, the mean wind erosion rates of *V. rotundifolia* ($6.02 \pm 0.09 \text{ g m}^{-2} \text{ s}^{-1}$) and *I. pes-caprae* ($5.91 \pm 0.11 \text{ g m}^{-2} \text{ s}^{-1}$) were at least 80% higher than that of *S. littoreus* ($3.29 \pm 0.05 \text{ g m}^{-2} \text{ s}^{-1}$), whereas under vegetation cover of 60%, wind erosion rates of *V. rotundifolia* ($1.71 \pm 0.05 \text{ g m}^{-2} \text{ s}^{-1}$) and *I. pes-caprae* ($1.09 \pm 0.04 \text{ g m}^{-2} \text{ s}^{-1}$) were at least 250% higher than that of *S. littoreus* ($0.31 \pm 0.02 \text{ g m}^{-2} \text{ s}^{-1}$) (Table 6). At a windward wind speed of $10.8 \pm 0.4 \text{ m s}^{-1}$ and vegetation cover of 20%, the mean wind erosion rates of *V. rotundifolia* ($9.14 \pm 0.12 \text{ g m}^{-2} \text{ s}^{-1}$) and *I. pes-caprae* ($8.25 \pm 0.08 \text{ g m}^{-2} \text{ s}^{-1}$) were at least 70% higher than that of *S. littoreus* ($4.75 \pm 0.09 \text{ g m}^{-2} \text{ s}^{-1}$), whereas under vegetation cover of 60%, wind erosion rates of *V. rotundifolia* ($2.09 \pm 0.07 \text{ g m}^{-2} \text{ s}^{-1}$) and *I. pes-caprae* ($1.58 \pm 0.05 \text{ g m}^{-2} \text{ s}^{-1}$) were at least 160% higher than that of *S. littoreus* ($0.59 \pm 0.05 \text{ g m}^{-2} \text{ s}^{-1}$) (Table 7). Collectively, these results clearly demonstrate that the grass *S. littoreus* has superior anti-wind erosion ability compared to *I. pes-caprae* and *V. rotundifolia* in reducing wind speed and wind erosion rate.

Table 4. Variation in leeward soil surface wind speeds under windward wind speed of $6.3 \pm 0.3 \text{ m s}^{-1}$ and different vegetation covers for the seedlings of the three foredune species.

Species	Leeward Soil Surface Wind Speed (m s^{-1})				
	Vegetation Cover				
	0%	20%	40%	60%	80%
<i>I. pes-caprae</i>	6.28 ± 0.32^a	4.58 ± 0.07^a	4.02 ± 0.05^b	3.24 ± 0.09^b	2.77 ± 0.04^b
<i>S. littoreus</i>	6.28 ± 0.32^a	4.15 ± 0.07^b	3.29 ± 0.04^c	2.52 ± 0.05^c	1.38 ± 0.06^c
<i>V. rotundifolia</i>	6.28 ± 0.32^a	4.63 ± 0.11^a	4.26 ± 0.04^a	3.63 ± 0.05^a	3.16 ± 0.06^a

Means \pm SDs for leeward soil surface wind speeds. Different superscript letters within the same column signify significant differences (Tukey's HSD post hoc testing) among species. N = 6. Significance level $p < 0.05$.

Table 5. Variation in leeward soil surface wind speeds under windward wind speed of $10.8 \pm 0.4 \text{ m s}^{-1}$ and different vegetation covers for the seedlings of the three foredune species.

Species	Leeward Soil Surface Wind Speed (m s^{-1})				
	Vegetation Cover				
	0%	20%	40%	60%	80%
<i>I. pes-caprae</i>	10.78 ± 0.47^a	6.55 ± 0.13^a	5.5 ± 0.12^a	4.89 ± 0.12^a	4.04 ± 0.08^a
<i>S. littoreus</i>	10.78 ± 0.47^a	5.79 ± 0.11^b	4.52 ± 0.06^c	3.86 ± 0.09^b	2.05 ± 0.09^b
<i>V. rotundifolia</i>	10.78 ± 0.47^a	6.43 ± 0.16^a	5.4 ± 0.08^a	4.82 ± 0.06^a	4.16 ± 0.05^a

Means \pm SDs for leeward soil surface wind speeds. Different superscript letters within the same column signify significant differences (Tukey's HSD post hoc testing) among species. N = 6. Significance level $p < 0.05$.

Table 6. Variation in wind erosion rates under windward wind speed of $6.3 \pm 0.3 \text{ m s}^{-1}$ and different vegetation covers for the seedlings of the three foredune species.

Species	Wind Erosion Rate ($\text{g m}^{-2} \text{ s}^{-1}$)				
	Vegetation Cover (%)				
	0%	20%	40%	60%	80%
<i>I. pes-caprae</i>	8.21 ± 0.29^a	5.91 ± 0.11^a	3.94 ± 0.04^b	1.09 ± 0.04^b	0.41 ± 0.06^b
<i>S. littoreus</i>	8.21 ± 0.29^a	3.29 ± 0.05^b	1.39 ± 0.04^c	0.31 ± 0.02^c	0.13 ± 0.01^c
<i>V. rotundifolia</i>	8.21 ± 0.29^a	6.02 ± 0.09^a	4.71 ± 0.08^a	1.71 ± 0.05^a	0.58 ± 0.05^a

Means \pm SDs for wind erosion rates. Different superscript letters within the same column signify significant differences (Tukey's HSD post hoc testing) among species. N = 6. Significance level $p < 0.05$.

Table 7. Variation in wind erosion rates under windward wind speed of $10.8 \pm 0.4 \text{ m s}^{-1}$ and different vegetation covers for the seedlings of the three foredune species.

Species	Wind Erosion Rate ($\text{g m}^{-2} \text{ s}^{-1}$)				
	Vegetation Cover (%)				
	0%	20%	40%	6%	80%
<i>I. pes-caprae</i>	12.56 ± 0.34^a	8.25 ± 0.08^b	5.96 ± 0.09^b	1.58 ± 0.05^b	0.69 ± 0.06^b
<i>S. littoreus</i>	12.56 ± 0.34^a	4.75 ± 0.09^c	2.48 ± 0.08^c	0.59 ± 0.05^c	0.22 ± 0.03^c
<i>V. rotundifolia</i>	12.56 ± 0.34^a	9.14 ± 0.12^a	6.64 ± 0.19^a	2.09 ± 0.07^a	0.99 ± 0.09^a

Means \pm SDs for wind erosion rates. Different superscript letters within the same column signify significant differences (Tukey's HSD post hoc testing) among species. N = 6. Significance level $p < 0.05$.

4. Discussion

4.1. Growth Characteristics

Our results revealed seedling growth characteristics varied significantly among the three foredune species. Most growth characteristics were significantly higher for *I. pes-caprae* seedlings than for

V. rotundifolia and *S. littoreus* seedlings. However, the number of root tips were similar among species. In sand dune area, plant growth is restricted, and sand can be eroded easily, causing another limitation for vegetation growth. Seedling growth of foredune plants is very important in coastal dune restoration. Restored vegetation serves as a stabilizing agent in dune ecosystems [11,12]. Previous reports indicated that seedlings with larger stem base diameter and greater biomass survive and grow better than smaller seedlings [38–40]. *I. pes-caprae*, *S. littoreus*, and *V. rotundifolia* are native foredune plants having important functions in sand dune stabilization and restoration. Overall, our results show that *I. pes-caprae* seedlings with better growth characteristics than *V. rotundifolia* and *S. littoreus* seedlings are more suitable for dune stabilization and ecosystem restoration in coastal areas.

The roots of *I. pes-caprae* (vine) and *S. littoreus* (grass) seedlings resemble M- (massive) type, while *V. rotundifolia* (shrub) seedlings show a VH- (vertical and horizontal) type root system, consistent with a previous study [13]. Earlier studies suggest that grasses and vines with fibrous roots can be utilized in soil and water conservation and slope stabilization [14,41]. Previous studies demonstrated that an M-type root is favorable for surface erosion control [42], whereas a VH-type root is advantageous for erosion control and slope protection [43,44]. Consequently, *I. pes-caprae* (vine) and *S. littoreus* (grass) with fibrous roots and M-type root systems are recommended for coastal front line mixed planting, while *V. rotundifolia* with a deep, woody taproot system is suggested for second line plantings. Our results also revealed that *I. pes-caprae* possesses deeper roots and longer total root length than *V. rotundifolia* and *S. littoreus*, suggesting better ability for nutrient acquisition and water uptake in foredune areas [45–48]. Thus, it implicates that *I. pes-caprae* is more competitive than *V. rotundifolia* and *S. littoreus* in this environment.

Our results also showed that all root morphological characteristics, except for specific root length, varied greatly among species. They were significantly higher for *I. pes-caprae* seedlings than for *V. rotundifolia* and *S. littoreus* seedlings. Previous studies have demonstrated that root growth characteristics significantly influence the acquisition of nutrients and water [49–51]. Wendling et al. [52] indicated that nutrient acquisition is closely related to root biomass, shoot biomass, and root tissue density. Moreover, root density, root tissue density, and total root surface area have significant effects on root anchorage and erosion control [53–55]. Along the sandy seashores in Taiwan, *I. pes-caprae*, *S. littoreus*, and *V. rotundifolia* form a dense mat on the sand dune [8–10]. Generally, native foredune pioneer plants have adaptations to withstand the harsh environmental conditions in coastal areas and are beneficial for sand dune rehabilitation. Taken together, our results show that *I. pes-caprae* seedlings have better root growth characteristics and are able to adapt better to the harsh conditions in the sand dune areas than other two species.

4.2. Plant Uprooting Resistance

The results on the uprooting tests demonstrated that the uprooting force of shrub *V. rotundifolia* is significantly higher than that of vine *I. pes-caprae* and grass *S. littoreus*. Regression analysis of uprooting force and growth characteristics shows strong positive correlations with height, root length, and root surface area. These results are congruent with previous studies [53,56,57]. In fact, *V. rotundifolia* with woody taproot and profuse lateral roots has higher uprooting resistance than *I. pes-caprae* and *S. littoreus* with fibrous roots. Moreover, it has been demonstrated that plants with long taproots and profuse lateral roots are better able to withstand erosion [54]. Altogether, *V. rotundifolia* has the highest uprooting resistance among the three species and is advantageous for sand dune stabilization.

4.3. Root Tensile Strength

Root tensile strength significantly affect the magnitude of root reinforcement in bioengineering [31,58–60]. Our analyses show that root tensile resistance and tensile strength are significantly different among species. Root tensile force was highest for *V. rotundifolia*, lower for *I. pes-caprae*, and lowest for *S. littoreus*, whereas root tensile strength of *S. littoreus* and *V. rotundifolia* was significantly higher than that of *I. pes-caprae*. There is a positive power law correlation between root diameter and tensile force,

consistent with the results of earlier studies [31,61–63]. In addition, root tensile strength increases with decreasing root diameter following a negative power law correlation, which is in agreement with previous studies [16,29,32,62,63]. Genet et al. [62] explained the relation as root cellulose content decreases with increasing root diameter. However, Zhang et al. [63] ascribed the relation to root cellulose percentage increases, alpha-cellulose percentage increases, and lignin percentage decreases with increasing root diameter. Further study is required to verify the root cellulose and lignin contents of these foredune plants.

4.4. Anti-wind Erosion Ability

Generally, foredune plants can reduce erosion by curtailing wind speed. Fore-dune plants, such as *I. pes-caprae*, *S. littoreus*, and *V. rotundifolia*, can withstand harsh conditions. They can prevent wind erosion by reducing the wind speed and trap wind-blown sand in the foredunes. This study highlights the significant effect of foredune vegetation on reduction of wind speed and wind erosion rate. Wind speed reduction for *S. littoreus* seedlings is significantly higher than that of *I. pes-caprae* and *V. rotundifolia* seedlings. Furthermore, wind erosion rate for *S. littoreus* seedlings is significantly lower than that of *I. pes-caprae* and *V. rotundifolia* seedlings. Earlier studies have indicated that vegetation cover can reduce wind speed and wind erosion [5,24,64]. Taken together, these findings clearly demonstrate that the anti-wind erosion ability of *S. littoreus* is the highest, that of *I. pes-caprae* is the second, and *V. rotundifolia* is the lowest. Tong and Lin [2] carried out a study on dune restoration during the typhoon season. Their results showed that vegetation of *I. pes-caprae* is severely affected by typhoons, whereas *S. littoreus* exhibits a strong ability to resist typhoons. It is surprising to find that *S. littoreus*, with hard culm and sparse tough spiny blades, has a better anti-wind erosion ability than *I. pes-caprae*, with sprawling vines and large coriaceous leaves. Further researches are required to investigate the effects of leaf and shoot morphological characteristics of these foredune plants on the reduction of wind speed and erosion rate.

Taken together, the rank order of species selection criteria for coastal sand dune conservation by vegetation planting is: Anti-wind erosion ability > growth performance > root characteristics > root biomechanical properties.

5. Conclusions

This study shows *I. pes-caprae* seedlings have significantly better growth characteristics than *V. rotundifolia* and *S. littoreus* seedlings. Root growth characteristics of *I. pes-caprae* seedlings are also significantly higher than that of *V. rotundifolia* and *S. littoreus* seedlings. Moreover, the uprooting resistance of *V. rotundifolia* seedlings is significantly higher than that of *S. littoreus* and *I. pes-caprae* seedlings. *S. littoreus* and *V. rotundifolia* seedlings have higher root tensile strength than *I. pes-caprae* seedlings. However, above all, wind tunnel tests demonstrate *S. littoreus* has superior anti-wind erosion ability than *I. pes-caprae* and *V. rotundifolia*. These findings highlight that the technology of coastal sand dune stabilization can be greatly improved by incorporating the knowledge of plant anti-wind erosion ability. It is recommended that plant species selection criteria for coastal sand dune stabilization is: Anti-wind erosion ability > growth performance > root characteristics > root biomechanical properties. Interestingly, *S. littoreus*, with hard culm and sparse tough spiny blades, has a better anti-wind erosion ability than *I. pes-caprae*, with sprawling vines and large coriaceous leaves. Further studies on the effects of leaf and shoot morphological traits of these foredune plants on the reduction of wind speed and erosion rate are needed. Taken as a whole, these results clearly demonstrate that *I. pes-caprae* and *S. littoreus* are beneficial for front line mixed planting, while *V. rotundifolia* is suitable for second line planting in coastal foredune areas. This increased understanding of foredune plants is useful for ecological engineering of sand dune stabilization. We also suggest that specific mixed planting techniques should be practiced, such as mixing with other native species of beach bean (*Canavalia rosea*), beach naupaka (*Scaevola sericea*), and beach silvertop (*Glehnia littoralis*) in order to enhance erosion protection and biodiversity as well as coastal resilience and sustainability.

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