Identifying trait-based tolerance to sediment dynamics during seedling establishment across eight mangrove species

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Abstract

Mechanical disturbance from waves and sediment dynamics is a key bottleneck to mangrove seedling establishment. Yet, how species vary in tolerance to sediment dynamics has not been quantified. We identified how tolerance to sediment dynamics differs for three mangrove propagule traits: propagule size, successional stage, and type of embryo development. We selected eight mangrove species growing in south China that vary from small seeds to large elongated propagules, pioneer to climax species, and non-viviparous to viviparous. In a mesocosm set-up, we applied bed level treatments to establishing seedlings: erosion, control, or accretion, by removing 2 cm, 0 cm, or adding 1 cm of sediment per week over 3 weeks. We measured seedling survival, shoot, and root lengths, and the critical erosion depth that leads toppling or dislodgement. We identified five relationships between seedling morphology and accretion and erosion thresholds: (1) tall (viviparous) propagules likely had highest accretion thresholds; (2) small pioneer propagules grew relatively fast to increase accretion thresholds; (3) there was a strong correlation between the erosion threshold and root length; and (4) climax species grew longest roots overall, (5) while pioneer species grew longer roots fast in response to sediment erosion. We identify distinct strategies for successful establishment in sediment dynamics that contribute to understanding mangrove zonation and underpin the importance of restoring diverse forests containing not just robust climax species, but also adaptable pioneers. Furthermore, this study reveals maximum shoot and root length as key determinants for seedling stability across species, providing a simple proxy for modeling establishment events.

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Additional Supporting Information may be found in the online version of this article.

Seedling establishment is a vital stage in a plant's life and a primary bottleneck to maintaining and establishing new forest biomass (Leck et al. 2008). Establishment of seedlings can be particularly challenging in environments with mechanical disturbances, such as sediment erosion or accretion in coastal marshes, sand dunes, and snowdrift areas (Facelli 2008; Friess et al. 2012). Though variable success in seedling establishment is a natural part of ecosystem functioning, it can limit access to key resources and services that societies rely on. Such is the case with mangrove forests, which provide critical ecosystem services at global (carbon storage) and local scales (fish nurseries, coastal flood defense; Lee et al. 2014). For optimal

functioning, mangrove forests need to have a certain minimal size, particularly when the consequences of size reduction are directly linked to human survival, such as when mangrove forests are used for flood defense, where a wider forest will reduce waves and water levels more effectively (Horstman et al. 2014; Cao et al. 2015; Suzuki et al. 2019). To rely on mangrove ecosystem services, it is important to predict and maintain forest presence via seedling establishment. Yet, there is currently limited knowledge available to develop reliable models that can predict seedling establishment and forest expansion (Bouma et al. 2014; Gijsman et al. 2021; Hu et al. 2021). If natural forest size is reduced too much, forest width can be increased through restoration efforts. However, such efforts are not always successful (Terrados et al. 1997; Ellison 1999; Erftemeijer and Lewis 2000; Primavera and Esteban 2008; Lee et al. 2019), often due to inadequate on-site knowledge of drivers affecting seedlings establishment like salinity, hydrology, and appropriate species composition (Kodikara et al. 2017*a*). Thus, it is important to understand what mangrove seedlings need for successful establishment for both modeling and restoration efforts.

While the impact of abiotic drivers such as salinity and inundation on seedling establishment has been studied for numerous mangrove species (Ball and Pidsley 1988; Ye et al. 2005; Krauss et al. 2008), impact of mechanical disturbance from sediment dynamics has only been quantified for two mangrove species, namely the pioneer species *Avicennia alba* and *Sonneratia alba* (Balke et al. 2013; but *see* Cao et al. 2018; Redelstein et al. 2018 for saltmarsh species). Natural forest expansion as well as restoration often take place at the forest fringe where seedlings are exposed to mechanical disturbance from tides, waves, and sediment dynamics (Balke et al. 2011, 2013; Chen et al. 2018). The latter can result in sediment accretion or erosion, with an order of magnitude of 1 cm d^{-1} in the pioneer zone (Hu et al. 2020), and strongly affect seedling survival (Terrados et al. 1997; Ellison 1999). Sediment erosion can expose a seedling's roots, potentially reducing seedling stability or even completely uprooting seedlings (Balke et al. 2011). Sediment accretion can result in partial or complete burial of seedlings, leading to etiolation and ultimately mortality (Maun 1998; Thampanya et al. 2002). Improving the knowledge of tolerance to these mechanical disturbances could improve restoration attempts and enable accurate predictions of future mangrove presence.

Balke et al. (2013) showed that there are large differences in tolerance to sediment dynamics between two pioneer species *A. alba* and *S. alba* that differ in traits like size and type of embryo development. It is likely that more such differences exist, as there are 72 mangrove species known to humankind, that vary in shape, type of embryo development, and successional stage (Tomlinson 2016), and range from tiny seeds weighing less than a milligram up to large, elongate propagules weighing up to 23 g (Wang et al. 2019). Moreover, some mangrove species are pioneers that survive well in the exposed

lower intertidal zone, whereas others are climax species that generally occur at less exposed, higher elevations (Friess et al. 2012). This can result in patterns such as observed between *Ceriops tagal* and *Rhizophora mucronata*, where the latter generally occur lower in the intertidal zone and establish root anchorage more quickly to overcome disturbance by waves (Robert et al. 2015). Following this, it is likely that tolerance to sediment dynamics will differ between the diverse group of mangrove species, and studying tolerance across species could advance our understanding in mangrove zonation and increase successful seedling establishment in the mangrove habitat.

Here, we aim to identify traits that contribute to successful establishment under sediment dynamics in the first month of a seedling's life, where we define trait in a broad sense, as a distinguishing quality or characteristic. We use a mesocosm experiment to create sediment accretion and erosion rates that are common in the forest fringe pioneer zone and measure how these treatments impact the growth and survival of eight mangrove species that co-occur in south China. The species cover a range of three propagule traits: successional stage (ranging from low-elevation pioneers to high-elevation climax species), propagule size, and type of embryo developments (non-viviparous, cryptoviviparous, or viviparous, where vivipary is the process where the embryo grows first out of the seed coat and then out of the fruit while still attached to the parent tree—or only the seed coat in the case of cryptovivipary; Tomlinson 2016). Specifically, we set out to learn if species have different accretion and erosion thresholds, and if the three traits provide an advantage in establishing in a sedimentary dynamic environment. For the three traits (successional stage, propagule size, and type of embryo development) we expect that being a pioneer, having a large propagule, and/or being viviparous respectively, contribute most to successful seedling establishment. By generating an extensive dataset, this research provides valuable new knowledge on seedling establishment in mechanically stressful environments.

Materials and methods

Species selection and traits

We selected eight mangrove species common in South China (Fig. 1): *Avicennia marina*, *Laguncularia racemosa*, *Sonneratia apetala*, *Aegiceras corniculatum*, *Rhizophora stylosa*, *Kandelia obovata*, *Bruguiera gymnorrhiza*, and *Bruguiera sexangula*. These species are native to the Pearl River Delta region in south China, with three exceptions: (1) *S. apetala* was introduced from Bangladesh for mangrove afforestation in the mid-1980s (Xin et al. 2013); (2) *L. racemosa* was introduced from Mexico in the early 2000s (Zhong et al. 2011); and (3) *B. sexangula* was introduced to Guangdong regionally but is common in the southern tropical areas, that is, Hainan island (Duke et al. 2010; GBIF 2021). We categorized each species for the following ordinal or quantitative traits:

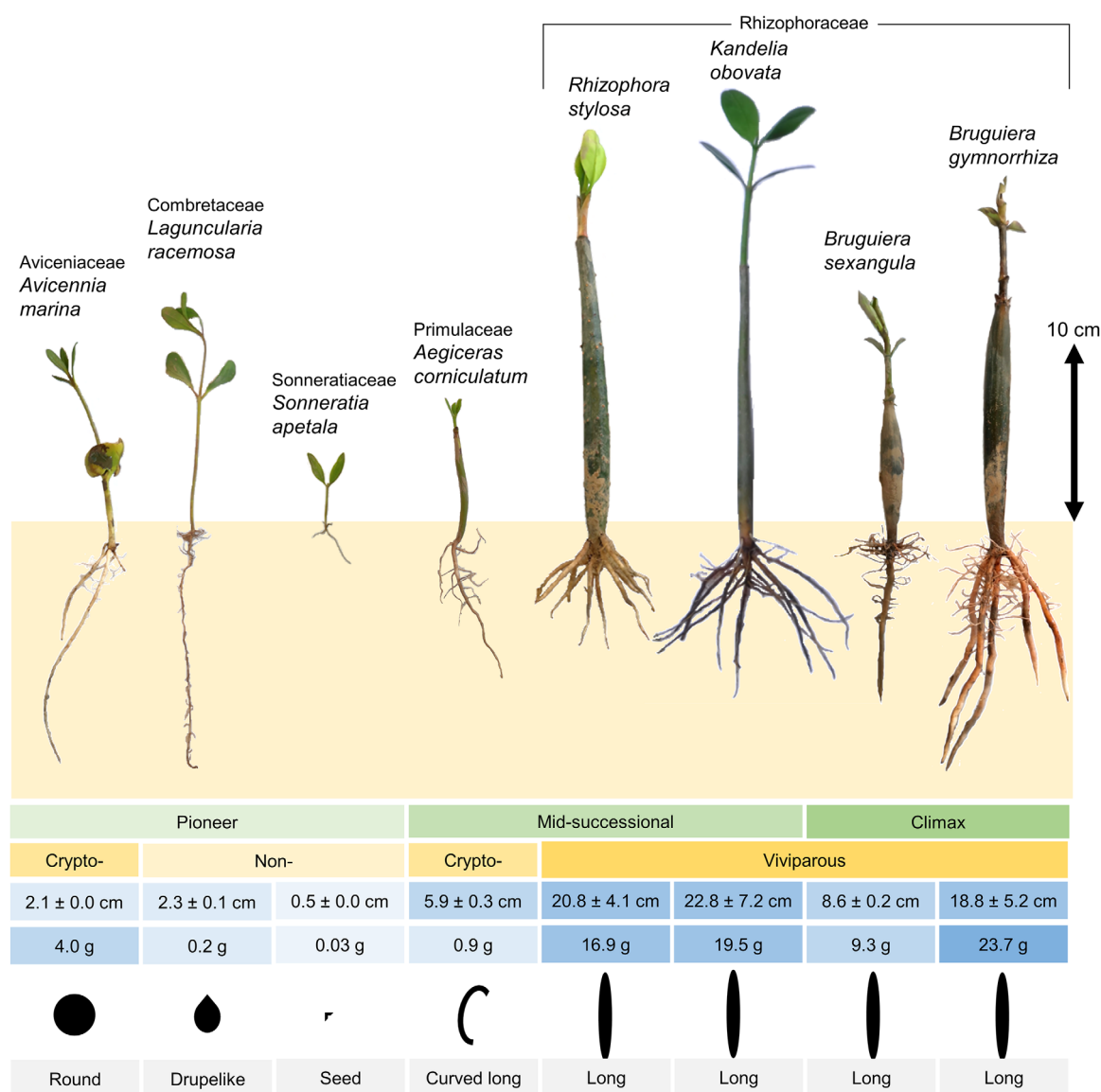- successional stage: pioneer, mid-successional, climax;

Fig. 1. Overview of species studied, with a photo (to scale) of a seedling that survived the experiment and a classification for each of the traits: successional stage, type of embryo development, propagule length (cm, mean ± variance), and propagule fresh weight (g, mean values from literature, variability can be found in Supplementary Table S1). For background information, propagule/seed shape is also shown (*not* to scale).

- type of embryo development: non-viviparous, crypto-viviparous, or viviparous;
- propagule size: length (cm) and fresh weight (g).

The species had diverging traits, such that we had at least two species in each trait group (Fig. 1; Supplementary Table S1).

Experimental design and growth conditions

The study was carried out in three phases, based on propagule availability. Each phase lasted 34 days. The first phase was carried out with *K. obovata* from 15 April 2019 – 19 May 2019, for which propagules were collected at the Guangzhou

Nansha Binhai Wetland, Guangdong, China 22°36′53.8″N 113°38′49.7″E in April 2019. The second phase was carried out with *L. racemosa*, *A. marina*, *R. stylosa*, *A. corniculatum*, *B. gymnorrhiza*, and *B. sexangula* from 19 July 2019 to 23 August 2019, for which propagules were collected at Hai Nan Dong Zhai Gang National Nature Reserve, Hainan, China (110°32′–110°37′E, 19°51′–20°1′N) in July 2019, and the third with *S. apetala* from 18 October 2019 to 21 November 2019, for which propagules were collected at 23°06′49.8″N 113°15′36.6″E in October 2019.

For each species and each sediment treatment, we used 12 replicates, so that we tested 288 seedlings in total: 8 species × 3 treatments × 12 replicates. Propagules were sowed on day

1 (Fig. 2) into pots filled with silty sediment (D50 = 8 μm) collected in the Pearl River Estuary at 22°36′19.6″N 113°35′52.3″E and at Qi'ao Island. The pots were placed in outdoor mesocosms that were constructed following the same method as in Balke et al. (2013; Supporting Information Fig. S1). We selected ripe propagules and, except for *S. apetala*, all propagules were sowed by gently pushing until 2.5 cm into the sediment to ensure they would not float up when inundation started (same depth as in Tomlinson and Cox 2000). Seedlings were watered daily with freshwater until inundation started. We used an alternative method for *S. apetala* because of complications we encountered with germination. Instead, ripe fruits were opened to extract seeds that were soaked in freshwater for 2 weeks; after this, we selected germinated seeds and planted them with their tiny root (0.5–3 mm) in the soil to avoid desiccation.

Seedlings were inundated twice daily for 2.5 hours each time (5 h d^{-1}) starting a week after sowing (Fig. 2). This inundation regime mimics a semidiurnal tidal cycle that is generally acceptable for mangroves (Lewis III and Estevez 1988; Yang et al. 2013), and is consistent with a similar experiment described in Balke et al. (2013). During inundation, water was still. Water had a salinity of 3 psu to allow all seedlings to germinate. This salinity was achieved by mixing water with salt to create artificial seawater. Mean water temperatures were 26.4°C in phase 1, 30.7°C in phase 2, and 22.6°C in phase 3.

Sediment treatments and critical erosion depth

Sediment treatments were applied 2, 3, and 4 weeks after sowing and carried out over 2 days due to labor intensiveness (Fig. 2). For erosion treatment, 2 cm was removed around seedlings, for control 0 cm, and for accretion treatment, 1 cm was added (cumulative −6, 0, and + 3 cm, respectively; *see* supplementary information 1.2). These sediment treatments were based on sediment dynamics generally found in the mangrove pioneer zone; a net change of about 1 cm week^{-1} (Hu et al. 2020). Initially, we opted for an erosion treatment

−1 cm per week but decided to change this to −2 cm during the first sediment treatment, because eroding only 1 cm was within the tolerance range of most seedlings and would not have resulted in useful results (i.e., all seedlings were likely to survive, which would make it hard to compare the effect of erosion between species). The extent of the sediment treatment could not be changed for the accretion treatment because this treatment required the pre-placement of discs before sowing (*see* Appendix S1), which was not possible anymore since the seedlings were already present in the pots. Shoot growth and seedling survival were measured twice per week. Shoot growth was measured from the top of the sediment layer to the tip of the plant. Survival was monitored by visually assessing the state of a seedling: alive, toppled, or dead. Plants that were considered toppled had fallen over thus far that they were resting on the side of the pot. As biological death did not occur, death was defined by the erosion treatment having removed sediment over the full length of the roots such that the seedling had become fully dislodged (and the seedling would float away when inundated), or the accretion treatment having completely buried a seedling and it did not re-emerge.

At the end of each experiment phase, a final test was carried out to measure critical erosion depth. We measured two types: toppling and dislodgement, as these might have different consequences for a seedling's survival (e.g., if a seedling is toppled its roots still have access to nutrients in the soil and may re-erect). Critical erosion depth (CED) was measured as follows: first, we subjected each seedling to a wave treatment by placing it in a flume with a water depth of 15 cm and generating waves with a wave height of 7–8 cm for approximately 1 min or 7 waves, such that the maximum wave orbital velocity was 0.26 m s^{-1} and the bed shear stress 0.26 Pa (Infantes et al. 2021; Supplementary Information 1.2). If the seedling did not topple, we removed a 0.5-cm layer of sediment and subjected the seedling to another wave treatment, until a seedling was toppled, upon which the erosion depth CED$_{topple}$ was
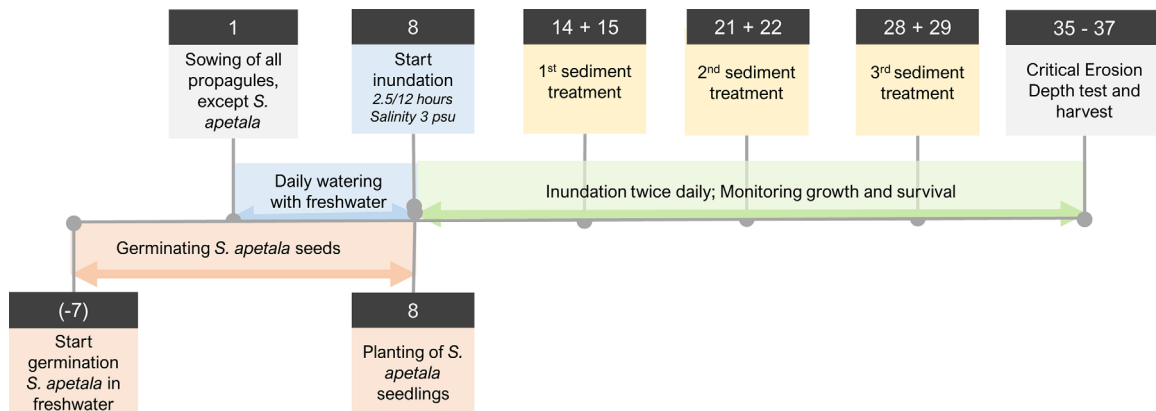

Fig. 2. Timeline showing on which days experimental steps were carried out. All three phases followed this timeline, where Day 1 started on 15 April, 19 July, and 18 October 2019. *S. apetala* was sowed in a different manner than the other species, hence the separate experimental steps.

noted. We then repeated the procedure again until a seedling was dislodged. When a seedling became dislodged, the erosion depth $CED_{dislodge}$ was again noted, as well as the number of roots and the maximum root length (length of the longest root) of the seedling, the latter which has been found to be a good predictor of seedling stability in previous studies (e.g., Balke et al. 2011).

Data analysis

We used survival analysis to analyze the differences in the survival data (alive, toppled, or dead) first between sediment treatments, and second between species. Survival data allow for the inclusion of right-censored data, meaning that the event of interest (toppled or dead) did not take place in the study time frame (Bland and Altman 1998). Data were analyzed twice using a Kaplan–Meier Mantel–Cox log-rank test, where we categorized toppling once as alive and once dead (R version 4.1.1—used in all data analyses—with package "survival" version 3.2.13), and we used a post hoc analysis to make pairwise comparisons between species (R package "survminer" version 0.4.9). The Kaplan–Meier Mantel–Cox log-rank test assumes that censoring is unrelated to study outcome, that events happened at the time specified, and that survival probabilities are the same for subjects that were added earlier or later to the study (Bland and Altman 2004). None of these assumptions were violated in our experimental set-up. We used ANCOVA with sediment treatment as the continuous variables, and species as a categorical variable to analyze differences between species and treatments for variables measured at the end of the experiment: maximum shoot length (cm), longest root length (cm), total shoot growth (cm), and relative shoot growth rate. We used a significance level of $\alpha = 0.05$ and set treatment as an interaction term, so that the effect of sediment treatment could vary between species.

Relative shoot growth rate ($cm\,d^{-1}$) was calculated as follows (Hoffmann and Poorter 2002)

$$(\ln H_1 - \ln H_0)/(t_1 - t_0) \qquad (1)$$

where H_0 is the initial propagule length (cm) at time t_0 (days) and H_1 is the maximum shoot length (cm) measured at the end of the experiment at time t_1 (days), which was Day 34. We used the absolute CED_{topple} and $CED_{dislodge}$ measurements to obtain net CED_{topple} and $CED_{dislodge}$ measurements: cumulative treatment + absolute CED = net CED (Balke et al. 2013), so that the CED of a seedling with a cumulative sediment removal of 6 cm could be compared to a seedling with a cumulative addition of 3 cm sediment.

We carried out Pearson correlations (with significance level $\alpha = 0.05$) to identify potentially relevant correlations between absolute and net CED_{topple} and $CED_{dislodge}$, seedling size (*maximum shoot length [cm], longest root length (cm), total shoot growth (cm), and relative shoot growth rate [cm d⁻¹]*), and traits (*successional stage, type of embryo development, and propagule length*

[cm] and fresh weight [g]). We then further analyzed the most relevant Pearson correlations (R package "corrplot" version 0.92).

Results

Survival and growth response to sediment treatments

Generally, seedling survival was more sensitive to sediment erosion than to accretion. For all species, significantly more seedlings died under erosion than accretion treatments (Fig. 3; Supplementary Tables S2, S3). In fact, all species survived accretion except the seedling of the small pioneer *S. apetala* (2/12 died) that had grown significantly shorter shoots than the other species over the course of the 34-day experiment (Fig. 3; Supplementary Tables S4, S5).

In the erosion treatment group, we observed significant differences between the survival and growth between the eight species (Figs. 3, 4; Supplementary Tables S2, S4). The pioneer species *A. marina* and *L. racemosa* had comparable survival outcomes (pairwise comparisons revealed no significant difference between Kaplan–Meier survival curves at $\alpha = 0.05$; Supplementary Table S2), with some seedlings toppled (17% and 42%, respectively), some dead (33% in both species), and some alive (50% and 25%, respectively; Fig. 3). Meanwhile, the pioneer *S. apetala* seedlings, that had the smallest seeds and grew the shortest roots (Figs. 1, 4), had significantly lower survival, as all seedlings died (Fig. 3; Supplementary Table S3). It is noted that the *S. apetala* seedlings grew in the relatively coldest experimental phase (22.6°C), as that is when the species is naturally establishing. This may have affected the root growth slightly (Supporting Information Fig. S2). Mid-successional species *R. stylosa* and *K. obovata* produced significantly more roots than other species, yet those roots were also shorter, significantly in the case of *R. stylosa* (Figs. 4, Supporting Information Fig. S6; Supplementary Table S5). Accordingly, they had similar, low survival outcomes, especially when toppling was assumed to be deadly (Fig. 3; no significant difference between Kaplan–Meier survival curves at $\alpha = 0.05$; Supplementary Table S3). The mid-successional *A. corniculatum* seedlings germinated too slowly and were eroded before growing anchoring roots (Fig. 3). The climax species *B. sexangula* and *B. gymnorhiza* had high survival outcomes (Fig. 3; Supplementary Table S3). In fact, *B. sexangula* survived all erosion treatments (Fig. 3). It also had the highest mean maximum root length (13.72 cm; Fig. 4; Supplementary Table S3). *B. gymnorhiza* had survival outcomes similar to *A. marina* and *L. racemosa* (Fig. 3; no significant difference between Kaplan–Meier survival curves at $\alpha = 0.05$; Supplementary Table S3). It also grew similar root lengths over the 34 d of the experiment (10.19 cm; Fig. 4; Supplementary Table S5). Root and shoot lengths of seedlings that died during the experiment can be found in Supporting Information Fig. S3.

Pioneer species *A. marina* and *L. racemosa* grew significantly longer roots under erosion; 0.61 and 0.92 cm per cm erosion, respectively (Supplementary Table S5). At the same time, we observed a significant decrease in relative shoot growth rate
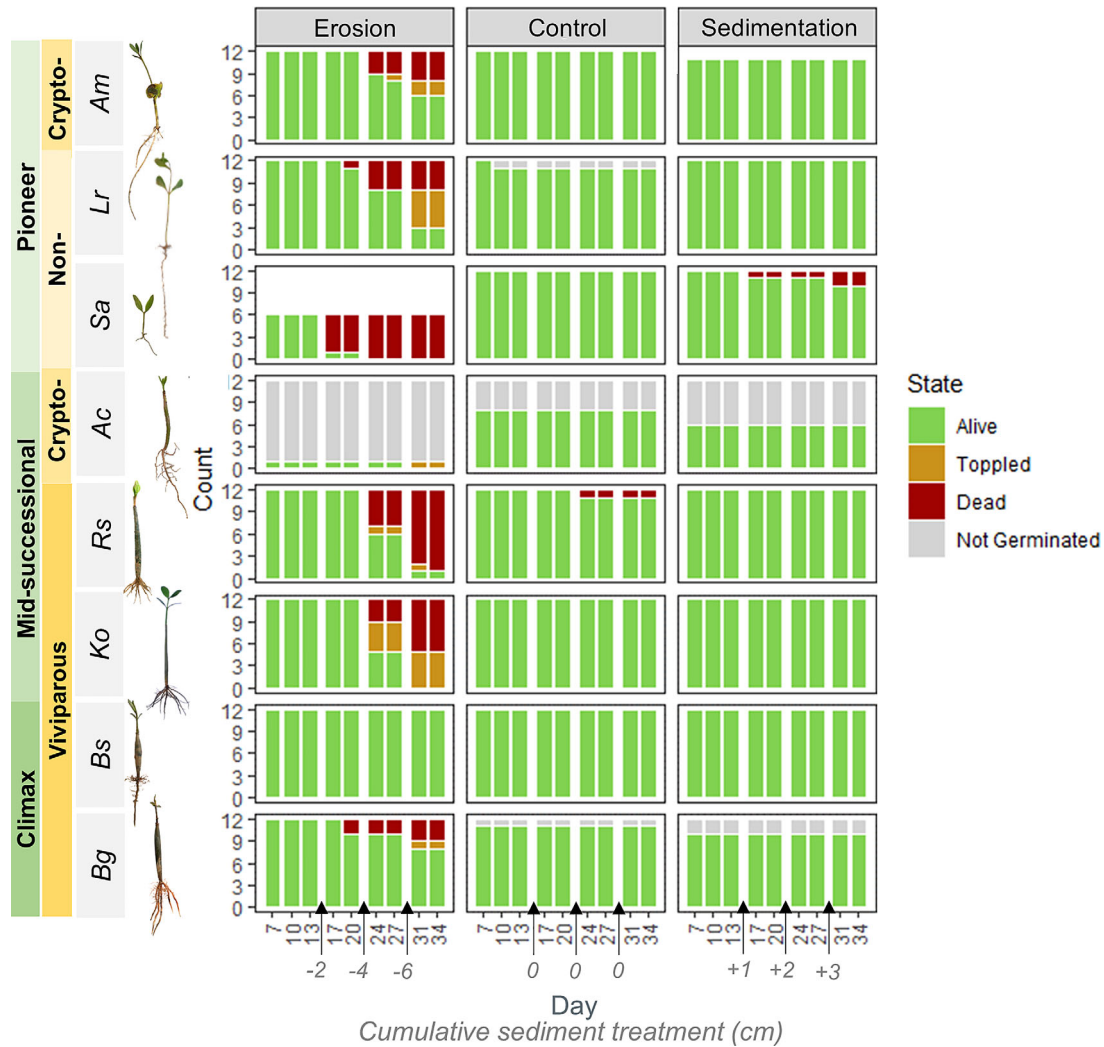
Fig. 3. Survival of the seedlings under the erosion, control, and accretion sediment treatments over the course of the 34-day experiment, with dotted vertical lines representing treatments (full timeline in Fig. 2). The traits successional stage and vivipary are indicated, and an image of a seedling of each species is shown, *not* to scale. Due to a lack of germinating *S. apetala* seedlings only six were tested in the erosion treatment. In the *A. marina* accretion group one seedling went missing. One *R. stylosa* seedling died in the control group for unknown reasons.

$(-0.02 \, \text{mm d}^{-1})$ toward sediment accretion in *A. marina* and *L. racemosa* (Supplementary Table S5). This may be because some seedlings of these pioneer species only developed roots in the accretion treatment groups. For the mid-successional *K. obovata* and climax seedlings *B. sexangula* and *B. gymnorrhiza*, we observed a significant increase in shoot length and relative shoot growth rate under accretion treatments (Fig. 4; Supplementary Table S5), though the positive pattern is less obvious for *K. obovata* in Fig. 4. Shoot growth over time can be found in Supporting Information Fig. S4.

Erosion tolerance correlates with root length

We identified a strong correlation between maximum root length and net $CED_{dislodge}$ across species ($r = 0.84$, $p < 0.01$; Figs. 5, 6a, Supplementary Figure S5). Interestingly, a

correlation between maximum root length and net CED_{topple} was much weaker ($r = 0.55$, $p < 0.01$; Figs. 5, 6b), suggesting a different mechanism driving CED_{topple} than $CED_{dislodge}$. There were weak significant negative correlations between the number of primary roots and net CED_{topple} and net $CED_{dislodge}$ (-0.17 and -0.42, respectively; Fig. 5), largely due to the significantly higher number of roots counted on the mid-successional *K. obovata* and *R. stylosa* seedlings (Supporting Information Fig. S6), which were not the most stable species (Fig. 4). When these two species were excluded, only a (weaker) significant correlation between the number of primary roots and net $CED_{dislodge}$ remained ($r = -0.27$, $p < 0.01$).

With maximum root length as a likely mechanical predictor of net $CED_{dislodge}$, we subsequently identified which trait
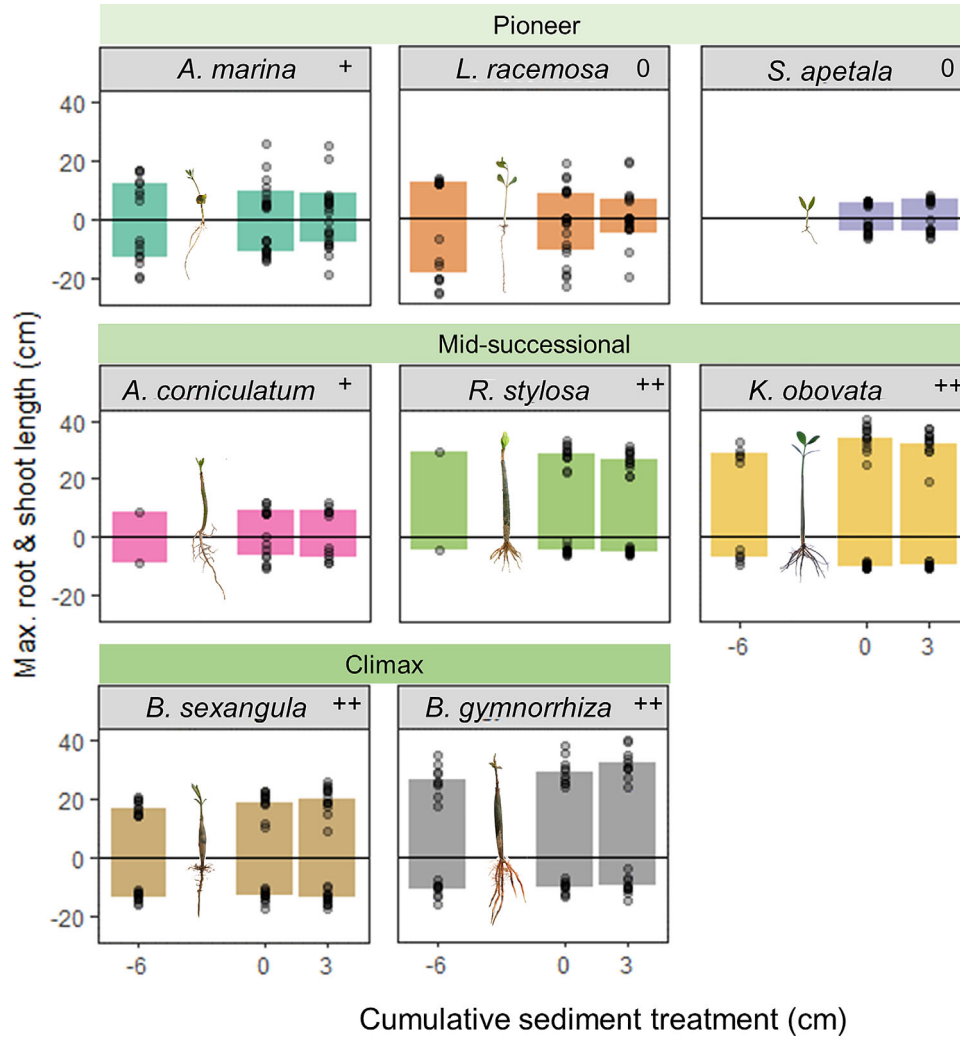
Fig. 4. Maximum shoot and root length of the surviving seedlings after 34 days under the erosion, control, and accretion sediment treatments, showing the means and underlying data of the shoot lengths and maximum root lengths (cm) for surviving seedlings of each species, where shoot length is depicted on the positive *y*-axis and root length on the negative *y*-axis. Successional stage is indicated and an image of a seedling of each species is shown, *not* to scale. Type of embryo development is indicated with 0 = non-viviparous, $+$ = cryptoviviparous, $++$ = viviparous.

correlated most with maximum root length. We found that successional stage best explained variation in maximum root length, which captures the strong response in maximum root length to sediment treatment in the pioneer species, compared to mid-successional and climax species (Fig. 7a). The pattern is not so apparent for the pioneer *S. apetala*, likely because we have no data for their root lengths in the erosion treatment. It is noted that although the pioneer species have higher root length plasticity under sediment erosion, the sediment erosion itself may lower their absolute $CED_{dislodge}$, canceling each other out if erosion is deeper than root length.

To find a better mechanical predictor for net CED_{topple} than only root length, we considered also shoot length (there was no significant collinearity between maximum root length and maximum shoot length; Fig. 5). Such a model explained the variation in the data slightly better (net $CED_{topple} \sim$ root: adj.

$R^2 = 0.27$, net $CED_{topple} \sim$ root + shoot: adj. $R^2 = 0.32$; Supporting Information Fig. S7a), indicating that toppling tolerance is possibly driven by above- and belowground seedling morphology. Alternatively, we considered the root/shoot ratio (maximum root length [cm]/shoot length [cm]), above and belowground oven-dried dry weight (g), and a below/aboveground ratio (Supporting Information Fig. S7). For those, we did not find significant correlations with net CED_{topple}. Because the mechanical predictor for net CED_{topple} was not so clear as it was for net $CED_{dislodge}$, we also analyzed the correlations between traits and net CED_{topple} directly (Fig. 5). We found that successional stage best explained variation in net CED_{topple}, where climax species had highest net CED_{topple} (Fig. 7b). Furthermore, net CED_{topple} had a stronger inverse correlation with sediment treatment (i.e., a more rapid increase in net CED_{topple} toward erosion) for pioneers
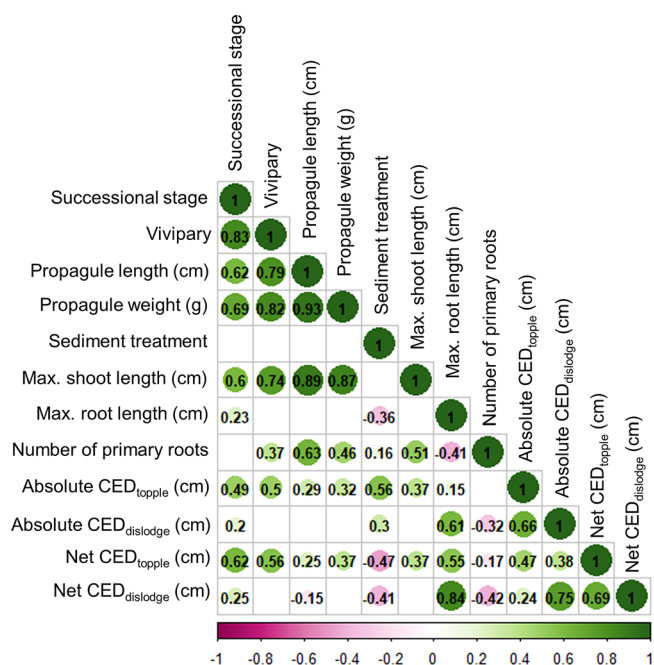
Fig. 5. Pearson correlations between propagule traits and the measurements of the surviving seedlings taken at the end of the experiment. Showing significant correlations only ($\alpha = 0.05$).

Shoot length correlates with propagule size

We analyzed which traits correlated most strongly with shoot length after 34 days of growth and found the strongest correlation with initial propagule length ($r = 0.89$, $p < 0.01$; Figs. 5, 8a), followed closely by propagule weight ($r = 0.87$; Fig. 5). We observed a significant negative, logarithmic correlation between relative shoot growth rate and propagule length ($y = 0.05 + \log(-0.002x)$, $r = -0.89$, $p < 0.01$; Fig. 8b), such that the smallest species grew relatively fastest. Absolute growth rate is shown in Supporting Information Fig. S8.

Discussion

Successful seedling establishment is essential to preserve and restore mangrove ecosystems and their services. Here, the impact of mechanical disturbance on mangrove seedling establishment is studied across a range of species diverging in the traits successional stage, type of embryo development, and propagule size. We found a key factor explaining successful seedling establishment under erosion was root length. Climax species had the longest roots overall, while the plasticity of pioneer species allowed them to develop longer roots in response to sediment erosion. Species with small propagules were found to be the most sensitive in that they were buried most easily. Overall, in our 34-day study sediment erosion was more challenging than accretion for mangrove seedling establishment.
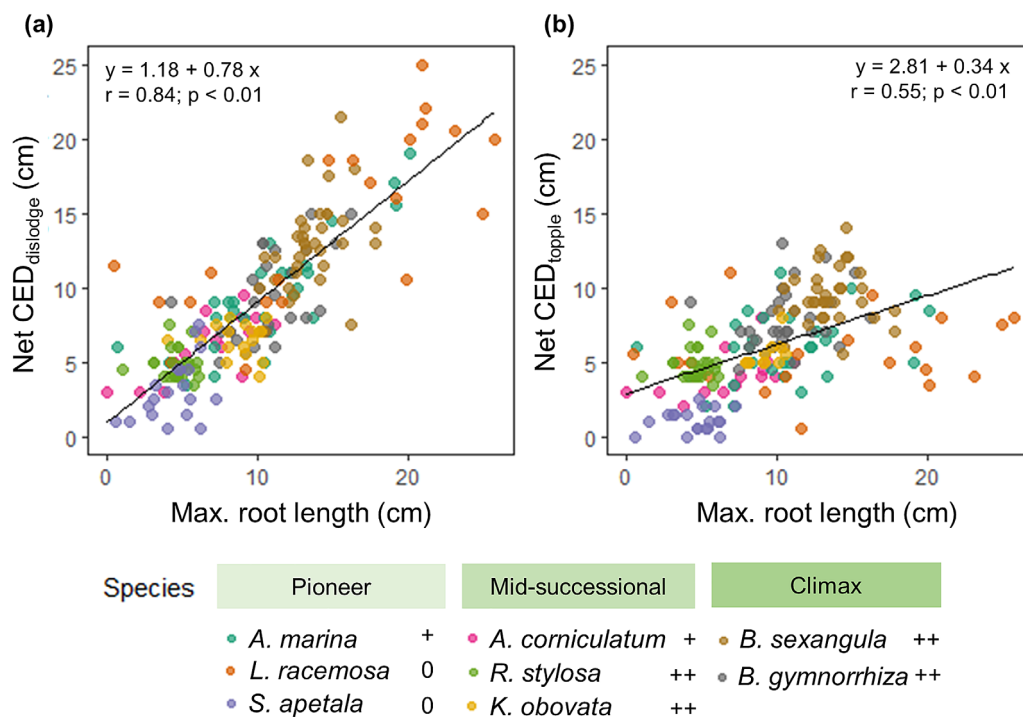
than for mid-successional and climax species, suggesting a morphological response beyond root length and dry weight (Fig. 7b).

Fig. 6. Critical erosion depth (CED) vs. maximum root length per treatment per species for **(a)** net CED$_{dislodge}$, **(b)** net CED$_{topple}$. Type of embryo development is indicated with $0 =$ non-viviparous, $+ =$ cryptoviviparous, $++ =$ viviparous.
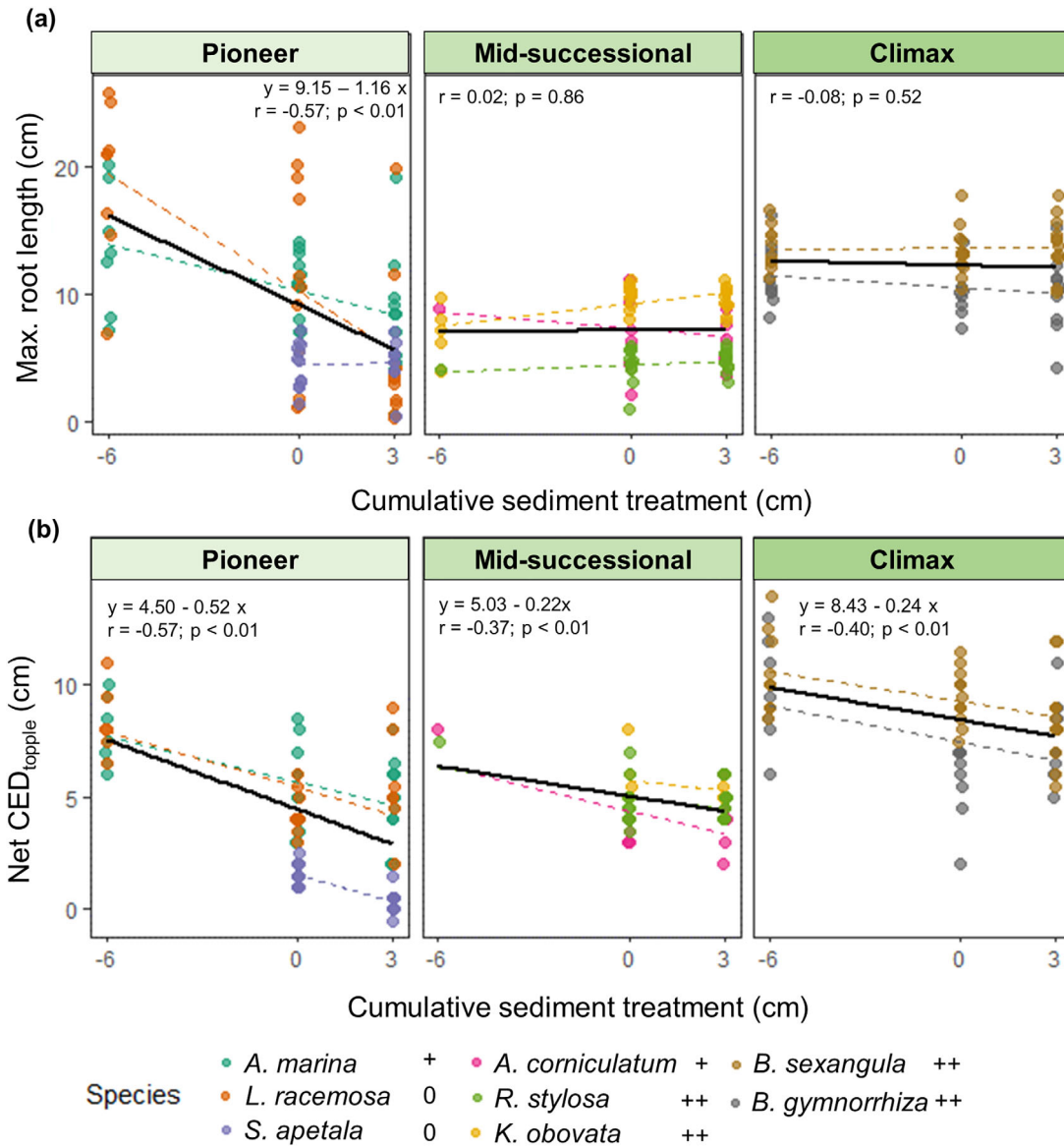
Fig. 7. Jitterplots of (**a**) maximum root length and (**b**) net CED$_{topple}$ at end of experiment per sediment treatment, shown per successional stage and per species. Black solid lines show correlations per successional stage, dashed colored lines show correlation per species.

Optimal seedling morphology and traits to withstand erosion and accretion

The Window of Opportunity framework on seedling establishment in sedimentary dynamic environments posed that seedlings need to grow fast enough to overcome mechanical disturbance from (1) tides; (2) waves; and (3) sediment dynamics (Balke et al. 2011, 2013). Here, we expand on this framework by showing how species with contrasting successional stages, type of embryo developments and propagule sizes, overcome accretion, and erosion thresholds by growing fast in general (i.e., regardless of sediment dynamics), being responsive to sediment dynamics or being already tall (Fig. 9).

Sediment erosion can have two consequences for a mangrove seedling: (1) loss of stability leading to toppling and (2) complete dislodgement. By analyzing more species than previous studies (Balke et al. 2011, 2013), we were able to reveal the optimal seedling morphology to overcome sediment erosion. Root length was a key morphological feature that had a strong correlation with critical dislodgement depth. In other words, propagules with long roots can withstand deeper erosion before being dislodged. Any deviation from this correlation between root length and dislodgement might be explained by waves pushing a seedling further out of the sediment than the erosion depth. That is, these simple seedling root systems do not hold a complex grip in the root-
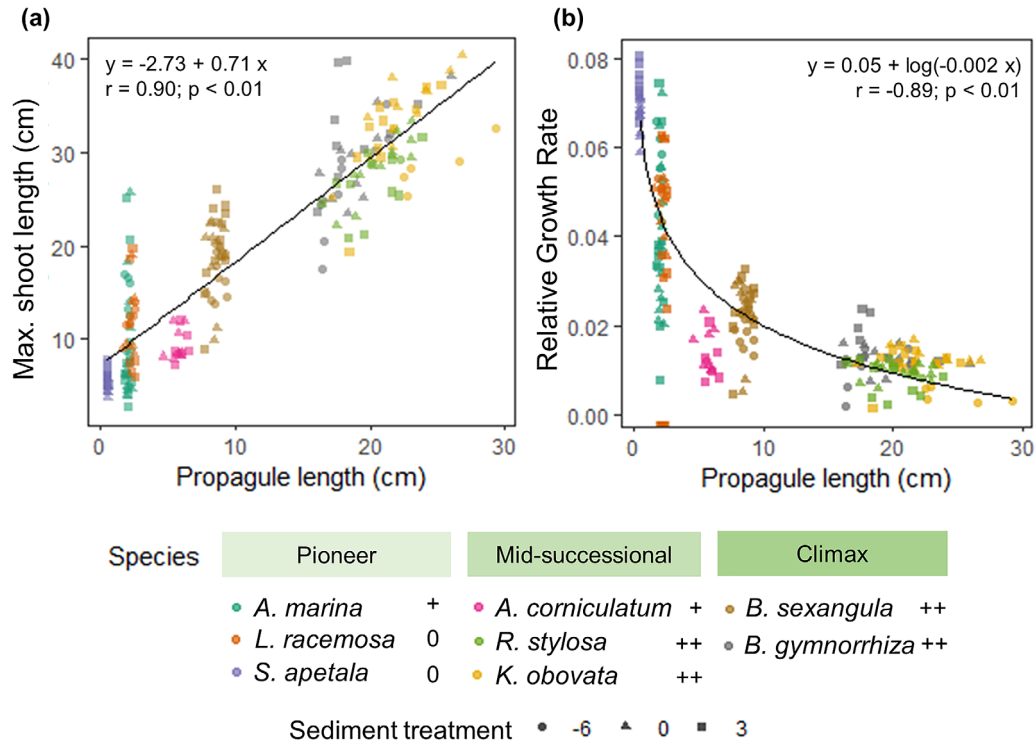
Fig. 8. (**a**) Shoot length at Day 34 and (**b**) relative growth rate of shoots, vs. propagule length, per species, per treatment. For the regression lines, treatments and species are pooled. Type of embryo development is indicated with 0 = non-viviparous, $+$ = cryptoviviparous, $++$ = viviparous.

sediment matrix (*see* Balke et al. 2011). The correlation with root length was however not so obvious for critical toppling depth. In fact, we argue that seedling stability is a function of not only belowground root morphology, but also aboveground shoot morphology. In our experiment, we found that critical toppling depth was better explained when we included both root and shoot length. Similarly, Redelstein et al. (2018) found a correlation between critical toppling depth, shoot biomass, and root biomass when they studied seedling stability in saltmarsh species. Research on the stability of mature trees in terrestrial ecosystems may explain our mangrove observations. Here, tall and inflexible trees will experience larger overturning moments than short and flexible trees (Urata et al. 2012; Sagi et al. 2019). For trees to remain stable, they need a wide, strong, and inflexible root system with a deep layer of heavy soil above it (Coutts 1983; Achim and Nicoll 2009). Though seedlings are much smaller than mature trees, the same physical laws apply. Thus, the most stable seedling would have small, short, and flexible shoots, and long and sturdy roots. Moreover, as water is denser than air, these morphological features that increase stability may be more important in aquatic systems (Bouma et al. 2005; Puijalon et al. 2011).

In terms of optimal morphology to avoid toppling or dislodgement, long roots were found in the pioneer species *A. marina* and *L. racemosa*, particularly in response to erosion

treatments. This responsiveness is likely a common feature in pioneer species, as increased biomass allocation to roots has also been observed in *A. alba* and *S. alba* after undergoing erosion treatments (Balke et al. 2013), and saltmarsh species developed longer roots compared to shoots after undergoing erosion treatments (Cao et al. 2018). Long roots were also found in the climax species *B. gymnorrhiza* and *B. sexangula*, which had highest survival in erosion treatments. The mid-successional species *K. obovata* and *R. stylosa* were less successful in developing long roots. Instead, they developed many short roots (Figs. 1, S6). At least in *R. stylosa*, but possibly also in *K. obovata*, this large number of roots is because their propagules abort their embryonic root and instead have many lateral, sub-apical root primordia (Tomlinson and Cox 2000). Perhaps these lateral root primordia are useful in earlier stages of seedling establishment, as a larger number of root primordia could provide more opportunities for a seedling to anchor and overcome disturbance from tides and waves (Balke et al. 2011). Furthermore, we found the shortest shoots in the pioneer species and in the mid-successional *A. corniculatum*. In pioneer species, we also expect highest flexibility. First, because increased flexibility in shoots has also been observed in pioneer mangrove and saltmarsh species in response to waves (Balke et al. 2013; Cao et al. 2020). Second, because we expect lower flexibility in species with long propagules, as these are quite rigid (Fig. 1). Although long, rigid viviparous

Fig. 9. Summary of ideal seedling morphologies for overcoming accretion and erosion thresholds, and the traits we identified that contribute to such a morphology. Blue arrows indicate hydrodynamic forcing. Asterisk (*) indicates expectations based on literature. Figure 1 shows the relevant traits for the eight species studied in this paper; here large viviparous propagules were *R. stylosa*, *K. obovata*, *B. sexangula*, and *B. gymnorrhiza*, *A. marina*, *L. racemosa*, and *S. apetala* were pioneers, of which *S. apetala* was the smallest, and *B. sexangula* and *B. gymnorrhiza* were climax species.

propagules are neither short nor flexible, they may avoid drag forces if they establish from a horizontal position. On the tidal flat, they have a roughly 50% chance of stranding horizontally, effectively reducing their length for a few weeks until they have grown upright (Supporting Information Figs. S9, S10; Tomlinson and Cox 2000).

Most seedlings survived accretion treatments, except for the tiny *S. apetala* seedlings. Thus, to avoid the risks of complete burial, it is best to be tall. Indeed, in a similar experiment with small *S. alba* seedlings and larger *A. alba* seedlings, the former had lower survival under sediment accretion (Balke et al. 2013). Seedlings with the tallest shoots after 34 days since sowing were among the species that had the tallest propagule (Fig. 8a). These species were all viviparous with long propagules, such that they were already initially tall—though only if they arrive vertically on the tidal flat (Supporting Information Figs. S9, S10). Shorter shoots were observed in the

species with smaller propagules, with the shortest shoots observed in *S. apetala*, which had the smallest propagules. To quickly achieve taller shoots as a small propagule, it needs to grow fast. Pioneer species grew relatively fastest, particularly in response to accretion. In many cases, accretion resulted in the tallest shoots observed. However, the mean shoot length of pioneers *A. marina* and *L. racemosa* reduced in accretion treatments because there were several individuals where the shoots failed to develop. In dune species, burial is known to reduce growth rates (Maun 1998), which may have happened here as well. More detailed studies that compare a larger range of accretion treatments, and thus burial depths, are needed to identify in detail how growth rate reduction and accretion thresholds depend on mangrove species traits. Such burial depths may need to be relative to the seedling height, such that each species can be tested for its response to complete burial. This could uncover wider species differences, such as

was observed by Thampanya et al. (2002), who found much higher survival and growth rates in *Sonneratia* species compared to *Avicennia* species (*A. officinalis* vs. *S. caseolaris*). Further burial studies could also include various (complete) burial durations. Complete burial can often be deadly (Maun 1998; Thampanya et al. 2002), but can be overcome. In dune species, on rare occasions, seedlings of species with large seeds can emerge from complete burial (Maun 1998). Furthermore, dune species can survive burial if erosion occurred within a few days after the burial event (Maun 1998). Cao et al. (2018) found similar results in experiments with saltmarsh species, which can survive higher levels of burial if bed levels fluctuate vs. a constant rate of burial. Studying various burial durations could reveal potential differences in species tolerances.

The current study works with a set range of environmental variables that result in growth rates specific to those environmental settings. However, it is well known that seedling growth rates are determined by a myriad of environmental drivers (Krauss et al. 2008), and the growth we observed in our experiment may differ widely in drier, more salty, darker, or otherwise different environments (e.g., Kodikara et al. 2017*b*; Sloey et al. 2022). This could result in shorter shoots or roots than we measured in our experiment and reduce erosion or accretion thresholds. To illustrate, in our study we used a semidiurnal inundation regime of 5 h d^{-1} in total. Previous work has shown that longer inundation can directly reduce establishment success under sediment dynamics (Balke et al. 2013). This could, for example, affect the relative shoot growth rate of *B. gymnorrhiza*, which is significantly reduced when growing in a waterlogged environment compared to *K. obovata*, so that *K. obovata* might produce deeper roots and reach higher erosion thresholds than *B. gymnorrhiz*a (Ye et al. 2003; previously *K. candel*; Sheue et al. 2003). Furthermore, our study was carried out across different seasons with different temperatures, because we used species whose propagules reach maturity in different seasons. Seasonal differences such as temperature can affect the growth rate of seedlings, and even within a season, or across years, different growth rates may be found (e.g., Gillis et al. 2019). Temperature difference may also have an impact on the erodibility of coastal sediment and the resulting critical erosion depth (Nguyen et al. 2019). Therefore, the effect of these and other environmental differences is worthy of further study in the context seedling establishment in sedimentary dynamic environments.

The main aim of the paper was to identify whether one of the traits, or a combination of traits, provides an advantage in establishing in a sedimentary dynamic environment. By doing so, we uncovered various strategies to overcome establishment thresholds in dynamic sedimentary environments (Fig. 9). We expected that being a pioneer would be advantageous to overcoming erosion and accretion thresholds. Indeed, pioneer species were responsive to erosion, and small pioneers grew relatively fast to avoid complete burial. We also expected that being viviparous would bring an advantage, and found that a

horizontal arrival on the tidal flat may potentially reduce the change of toppling. Furthermore, we expected that having a large propagule would be an advantage, and found that large propagules had taller shoots at the end of our experiment. Additionally, our findings contribute to our understanding of what makes pioneer species a pioneer. We initially assigned pioneer status based on location in the intertidal zone in south China, and being described as such in the literature (Supplementary Table S1). Now, we may add that being able to grow roots fast under erosion and, at least in the case of small propagule (*S. apetala*) being able to grow shoots fast under accretion, likely contribute to what makes them successful at growing in the pioneer zone.

Implications for mangrove restoration and modeling of mangrove establishment

Although in our study *Bruguiera*-like climax species were most robust with longest roots and tallest shoots, pioneers were most plastic in response to their environment and were hence also able to reach high root and shoot maxima. Furthermore, pioneer species typically have higher fecundity than climax species (Friess et al. 2012), and smaller propagules that allow them to disperse further away from the mature mangrove forest (Van der Stocken et al. 2015). This provides pioneer species with a larger number of offspring reaching colonizable land. Thus, a lower survival rate at the individual level, may make pioneers seem less successful than they really are. Hence it is useful to mix a broad range of species in restoration projects, especially in exposed sites, but keeping in mind that the inundation frequency should match the successional stage of the species. By including multiple species with diverse traits, the risk of establishment failure is mitigated by the presence of diverse establishment strategies.

We argue that the development of the shoot length and root length over time can be used as simple proxies to predict seedling survival in sedimentary dynamic environments. Identifying such simple proxies is valuable for modeling establishment events and restoration measures under global change. This kind of mechanistic modeling approach has for example recently been applied to predict the sensitivity of saltmarsh establishment under global and local stressors (Hu et al. 2021). Using such a mechanistic approach could support the prediction of seedling establishment beyond the limitations of the environmental setting of the current study. Including other factors than sediment dynamics, such as salinity, temperature, and light availability can be easily done, by using existing relations between such factors and how they affect the growth rate of seedling roots and shoots (reviewed in Krauss et al. 2008).

Data availability statement

The presented data can be found at 10.4121/19941527.

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Conflict of Interest

None declared.